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Stylops was chosen for the Congress Crest because of its association with the Rev. William Kirby who first described the Stresiptera. Kirby is sometimes called "the father of British Entomology" and was the first Honorary President of the Royal Entomological Society of London, the host Society of the Congress. *Stylops* also appears on the Society's seal.

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INAUGURAL PLENARY SESSION

At the Royal Albert Hall, on Wednesday, 8th July, 1964, when members of Congress were welcomed on behalf of Her Majesty's Government by Rt. Hon. Robert Carr, M.P., Secretary for Technical Co-operation.

PRESIDENTIAL ADDRESS

Professor O. W. Richards

Ladies and Gentlemen, it is with much pleasure that I declare open the 12th International Congress of Entomology and welcome you to England, to London, and to Imperial College.

Mesdames, Messieurs, ce m'est un grand plaisir de déclarer ouvert le douzième Congrès d'Entomologie Internationale et de vous faire les bienvenues en Angleterre, à Londres et à l'Imperial College.

Meine Damen und Herren, Es macht mir grosse Freude den zwölften internationalen Kongress der Entomologie zu eröffnen und zie herzlich willkommen zu heissen in England, in London und in Imperial College.

I fear that my knowledge of foreign languages is a small and shallow stream which soon runs dry and that I shall have to make the rest of this speech in English.

This is the first time I think, that one of our congresses has been held for a second time in one country. There is a special interest therefore in comparing the present congress with the one which was held at Oxford in 1912. The most obvious difference is that the present congress is much larger. The membership in 1912 included various corporate bodies such as societies and libraries, and various permanent members who did not actually attend, but it seems that only 147 entomologists were actually present in Oxford. On this occasion there are at least ten times as many full members. Amateur entomologists played a much larger part in that congress than they do to-day; in this country, at least, the subject was only just beginning to be professionalised. Finally, there has been a great change of emphasis in the branches of our subject which are studied. In 1912, insect physiology was little studied and there was relatively little of an explicitly ecological nature.

The increase in size of entomological congresses, especially since the war is far from being an unmixed blessing. We all like to meet our friends but the meeting is sometimes more

enjoyable and profitable if they do not all come on the same day. Of course, the only important objections to large congresses are the practical difficulties. There are very few places in England where it is possible to have a large scientific congress and this summer there are at least four different international congresses in this country. A congress which is too large tends to become self-defeating—it is difficult to find one's friends and several interesting topics are always being discussed simultaneously. The alternative approach is to have specialised symposia, sometimes made up of invited participants alone. For certain purposes these are no doubt very successful but I feel that we must continue to regard entomology as a single subject in which it is still possible for one man to take a broad interest. The International Congress of Entomology is one of the last strongholds of this outlook and it will be a great pity if it is ever lost completely.

Nevertheless, if we decide to organise a gathering of entomologists of all types from all over the world we must expect their numbers to be large and the range of topics discussed to be very wide. Moreover, many entomologists besides those invited to take part in organised discussions will wish to communicate papers. At the present Congress more than 750 papers are being offered. These have to be organised into a number of sections and published, in some form at least, in our Proceedings after the Congress is over.

The division of entomology into sections is a controversial subject on which universal agreement can hardly be expected. There are certain limiting factors of a practical nature which tend to override the demands of mere logic. However hard we work, no one section can listen to more than a hundred communications in a week unless there are parallel simultaneous sessions. Such an arrangement, however, is a *reductio ad absurdum* of the whole idea of sections which is to allow people with common interests to have a common programme of discussion. One must therefore either limit the number of communications or increase the number of sections. If we increase the number of sections too much we have the same difficulty that too many sessions must be held simultaneously. It is also necessary to find in the host country workers who have the knowledge to organise each section and this also may partly limit the sub-division of the subject.

More than a third of Congress funds are spent on publishing and distributing the Proceedings, even when the published account of each communication is kept as brief as possible. The permanent committee of the Congress has for some time been concerned with this problem and it is in fact part of a much more general difficulty. Scientific journals and literature of all kinds have proliferated since the war. The publications of congresses and symposia have become more numerous and have tended to become longer. The Royal Society in London recently considered this problem (1962, Sir Lindor Brown, Nature, 193: 724-5) and their advice was to cut down the amount of such publication, particularly where the material was in any case being published more fully elsewhere.

We all know that it may be much easier to obtain leave and financial support to attend a congress if a paper is being read there, so that there is a very natural pressure from those who wish to make formal communications. While the informal and social part of congresses are very important, one can hardly imagine a congress in which formal communications did not play a considerable part. But perhaps there is no reason why more than a short resumé should be published of most of the papers. Both to save our financial resources and to reduce the amount of scientific publications we have strong reasons to keep our Proceedings as short as we can. This can only be done by restricting the numbers of papers or better by making these that are published shorter. I feel that this sounds ungracious but the only other solution which would be a large increase in the membership subscription would be even less acceptable.

One of the most striking differences between the present Congress and the one which was held in England fifty years ago is the change in the emphasis given to different branches of entomology. At the Oxford Congress nearly half the papers fell in the field of taxonomy and morphology; one fifth of them were concerned with applied entomology. There was really no physiology and very little explicit ecology, the word at that date being hardly known to zoologists. At the present congress what may be broadly called "Agricultural Entomology", Medical Entomology and Ecology provide the largest groups of papers and insect physiology is a flourishing subject.

I don't think there has been any real reduction in the importance of insect taxonomy but

people are perhaps less ready to regard its details as suitable for public discussion. The growth of ecology is partly a matter of nomenclature. What might earlier have been called natural history is now often called ecology but there has been a very important development in population ecology which is almost entirely modern. These changes in the amount of attention which is paid to different branches of entomology are the chief reason why it is necessary to consider very carefully the sections into which the congress is organised. There is no necessary reason why the same sections should be retained in perpetuity.

When discussing plans for the present Congress we considered that the number of papers on various topics which had been offered at the last two or three congresses was an indication of the importance which should be assigned to them. If a topic has not recently been discussed in many communications it is possible that it is better regarded as a specialised branch of some wider subject. Other topics, such as the honeybee or social insects, now have separate international meetings devoted to them alone. It may well be that in future congresses, on the other hand, Applied Entomology and Ecology will have to be further sub-divided. Of course, the boundaries between different branches of entomology are rarely clearly defined but this difficulty can be met by having a number of joint sessions between two or more sections, as we are going to have on this occasion.

There are two other matters to which I will refer briefly. The first relates to the time-table of our sessions. The longer our sessions are and the more of them that are held simultaneously, the more important it becomes that we should adhere to our time-table. We hope therefore that the chairman of every meeting will endeavour to arrange that each paper starts and ends at the agreed time. Only in this way is it possible for our members to attend parts of different sessions, as many wish to do.

The second point concerns the social life of the Congress. Lounges in which members may sit and talk are available on the ground floor of the Beit Quadrangle (the part of the College near to the Albert Hall) and in the building on the south side of Prince's Gardens. We would like to provide more space of this kind but some rooms must be left for the non-entomological members of the College and suitable rooms are not yet all built. We are, however, placing chairs on the terraces surrounding the Beit Quadrangle and if the weather is fine we hope that these will prove useful.

I would like finally to assure you that the organisation of the present Congress has been arrived at only after a great deal of thought and discussion. The plans finally adopted have been a compromise between what has traditionally been done in the past, what would seem most logical at the present day, and what resources of men, money, space and time were actually available. I believe I am correct in saying that all papers offered by members of Congress early enough to appear in the printed programme have been accepted, though the times allotted to them and the length at which they will be printed in our Proceedings may be shorter than some members would have liked. The Organising Committee of the Congress very much hope that you will enjoy your stay in England and that you will find our sessions both profitable and enjoyable.

INAUGURAL ADDRESS

FIFTY YEARS OF INSECT PHYSIOLOGY

Sir Vincent Wigglesworth

The First international congress of entomology to be held in this country took place at Oxford just over half a century ago. I did not attend on that occasion. I was too busy collecting insects in the countryside. Born in the North, in Lancashire, my parents had moved South, to Hertfordshire in 1911. For me it was like discovering El Dorado—so rich in insect life were the lanes and woods of Hertfordshire in those days. (How different to-day, when industry and suburbia are sweeping everything before them).

I had already been passionately interested in insects for a good many years. Indeed, some years earlier in 1905 while caring for my culture of *Abraxas grossulariata*, I had discovered the metamorphosis of insects. In those days of uncorrupted youth it did not trouble me at all to learn, much later, that the phenomenon had already been described by Aristotle long before and that I could not claim "priority".

Before that, I had made an observation which had impressed me even more forcibly. We had in the garden in Lancashire a willow tree; and I was particularly attracted by the red galls of *Pontania* which it always carried in large numbers on its leaves. I opened these galls and found that every one contained a grub—although there was never any hole by which it could have entered. I sought the guidance of my parents about this mystery—but in vain. From that moment I was a committed entomologist.

Time passed; the collecting of insects continued; in 1918 I was able to watch *Papilio machaon* on the slopes of Vimy Ridge. Then in 1919, to Cambridge, with all available time spent collecting on the chalk hills and in the fens. While starting research in biochemistry under Professor Gowland Hopkins I was able, as a side-line, to look again at the pigments in the wings of *Pieris*. At that time Hopkins still believed the white pigment to be uric acid itself. I showed that about half the nitrogen excreted during pupal development was deposited in the wing-scales.

Dr. Erich Becker, whose early death was such a loss to insect biochemistry in Germany, described this work of mine as a "warnender Beispiel"—because I had estimated as uric acid what was proved a few years later to be the pterine pigment "leucopterine". But only last year, a colleague of mine, using modern methods was able to prove that in the Pierid butterflies the pterine pigments are indeed a major medium of nitrogen excretion, which is chiefly deposited in the wings. The pigments are indeed, as Hopkins had claimed, "waste substances which function in ornament".

In 1926 Professor P. A. Buxton was appointed head of the Department of Medical Entomology at the London School of Hygiene and Tropical Medicine. Buxton had formed the opinion that the future development of applied entomology required an intensive study of the physiology of insects. At that time I had just qualified in medicine and was invited to join Professor Buxton and work in this field.

My first discovery, in an incubator in the laboratory, was the blood-sucking bug *Rhodnius prolixus*, which had been brought from Venezuela by Professor E. Brumpt a year or two earlier and presented to Col. Alcock, Buxton's predecessor. *Rhodnius* proved to be a most valuable experimental animal; cultures of this insect, nearly all of them from Prof. Brumpt's strain, now exist in laboratories all over the world.

It is not my intention to recall the various lines of research into the physiology of insects which have occupied my time so happily since then. But in the course of these researches I have had to read pretty extensively in the literature of the subject and I have followed pretty closely the developments during the past forty years.

People sometimes speak as though almost all that is known of the physiology of insects has been gained in the last fifty years. But at the time of the Congress in 1912 there was a substantial body of knowledge in existence; indeed the main outlines of the subject had been mapped out. In 1910 Paul Marchal had written his admirable account of insect physiology

for Richet's *Dictionnaire de Physiologie*. Some of the insect chapters of Winterstein's *Handbuch der vergleichenden Physiologie* and some of the physiological sections of Schröder's *Handbuch der Entomologie* had already appeared. The foundations of our modern knowledge on insect respiration and digestion had been laid by F. Plateau forty years earlier. Early in the nineteenth century George Newport in this country had abandoned surgery to devote himself to insect physiology and in 1837 had published his classic work on the circulatory system of *Sphinx ligustri*. There was much good physiology in *Die Insekten* of V. Graber published in 1877. There are valuable contributions to the physiology of insects in the writings of Henri Fabre. The classic account of the optics of the insect eye, published by Exner in 1891, has begun to be questioned only during the last few years.

The main outlines of the sensory physiology of bees and ants (the perception of ultra-violet light, the training to colours, and the use of scent trails and solar navigation) had been marked out by those two remarkable amateurs of entomology, Sir John Lubbock in this country and, later, Auguste Forel in Switzerland. But Professor v. Frisch was still concerning himself with the behaviour of fishes; he had scarcely discovered his true vocation. Lubbock's classic little book on the metamorphosis of insects, first published in 1869, is still worth reading, but in 1912 the attempts to describe the physiological mechanism of the process were wholly speculative. Genetics had been established as a discipline since 1900; but the link between genetics and development had not yet been forged by Richard Goldschmidt. Entwicklungs-Mechanik of sea urchins and amphibia had been making rapid progress, and in 1908 R. W. Hegner, of the University of Michigan had made the first key discovery in the Entwicklungs-Mechanik of insects by proving the existence of "germ cell determinants" at the posterior pole of the egg of *Leptinotarsa*, which determine the cleavage cells arriving in that area to become the precursors of the gonads.

The discoveries of the fifty years that have passed since that time have been remarkable indeed. I do not propose to fill up my allotted time in giving you a complete catalogue of those advances. I would rather try to present a picture of the great change that has come about by the description of a few selected examples.

There are certain aspects of the physiology of insects that are peculiar to the Class, or at least to the Arthropoda. The first example that I wish to discuss is the tracheal system of respiration. It was pointed out by Thomas Graham, when he described the laws of gaseous diffusion in 1833, that insects must depend for their respiration on the diffusion of gases within the tracheal system. But it was not until 1921 that August Krogh in Copenhagen proved this idea experimentally, and by measurement and calculation.

Krogh's treatment of the subject was based on the assumption that the spiracles were always open. It is curious to reflect that at that time the importance of the spiracular valves in preventing the loss of water by the insect was not recognised.

We know now that if the spiracles are kept open the insect very soon dies of desiccation. This function was first pointed out by E. H. Hazelhoff in 1926 when studying under Hermann Jordan in Utrecht. In those insects which have no forced ventilation of the tracheal system the opening and closing of the spiracles represents a compromise between the need to obtain oxygen and the need to conserve water.

In the more active insects, as has been known since Plateau and earlier, there is an active mechanical ventilation of the system superimposed on simple diffusion. The directed streams of air, which were argued about during the last century, have been clearly demonstrated. And in the most recent publications the supply of oxygen from the tracheoles to the tissues has been studied quantitatively and it has been proved that here also diffusion is adequate to meet the respiratory needs even in the most active organs.

Following closely upon the realisation of the function of the spiracles in retaining water, came the recognition (in the late twenties) of the paramount importance of the waterproof properties of the integument. Odier in 1823 had discovered chitin in the insect cuticle. Odier made use of the elytra of *Melolontha* for his researches. He recognised that the horny substance of the elytron was an "albuminoid" material which had to be dispersed with hot alkali in order to liberate the soft and colourless chitin.

But this clear picture of the cuticle became lost in the course of the century, and the horny component itself came to be regarded as a sort of chitin. It was not until 1940 that this

brown material was recognised as a proteinaceous polymer in which the protein chains had been tanned and bound together by reaction with quinones.

This remarkable polymer, called "sclerotin", forms a striking parallel with "keratin", the corresponding polymer of vertebrates in which the protein chains are linked together through disulphide bridges. The recognition of the nature of sclerotin has added enormously to our understanding of the physiology of insects. And along with the discovery of sclerotin has come the recognition that neither chitin nor sclerotin is responsible for waterproofing the insect, but a third, waxy component, which crystallises out over the surface of the cuticle and forms a mechanical barrier to the escape of water molecules.

It is not possible to claim that the insect cuticle is fully understood. Far from it. But even in our present state of knowledge it has been revealed as a structure of great interest and enormous complexity.

It is a little surprising how slow we were to recognise the over-riding necessity for water conservation in the small terrestrial insect, as reflected in the rigorous closure of the spiracles and the waterproofing of the integument. Likewise, water must be conserved in the excretory and alimentary systems. The "rectal glands" which had seemed such puzzling structures in the past were obviously concerned, in many insects, in recovering the precious water from the excrement before it was discharged.

But rectal glands may be conspicuously developed also in insects with copious watery excreta. That has been proved to mean that they are also actively engaged in recovering valuable inorganic ions.

Thus we have been forced to abandon the simple picture of a process of excretion limited to the vasa varicosa of Malpighi, and to substitute for it an excretory *system*, in which the re-absorptive properties of the rectum are at least as important as the eliminating functions of the Malpighian tubules. This co-operative activity finds its highest development in the cryptonephridial system of beetles from dry environments.

So urgent is the need for inorganic salts, in animals living in fresh water, that, as Krogh discovered, many aquatic species have special organs for extracting chlorides, sodium, and potassium, from fresh water. The equivalent structures in the larvae of mosquitos and other Diptera proved to be the puzzling anal papillae, working in co-operation with the rectal epithelium.

I wish to turn now to a totally different side of insect physiology: the sense organs. Although many of the principles involved in the operation of insect sense organs, notably in the generation of the electrical nerve impulses, seem to be identical in insects and in vertebrates, there are certain features that are peculiar to the insects.

For nearly a century and a half we have been content with the mosaic theory of vision by the compound eye as put forward by Johannes Müller and later developed by Exner. But during the last few years the theory of image formation by the compound eye has entered once more into a state of flux. I cannot elaborate the matter here, but if I might hazard a guess it would be that the mosaic theory will continue to stand, but at the same time it is becoming clear that this is not the only way in which the compound eye can be used. A certain amount of visual analysis can take place within the single ommatidium—in the flicker created by radial patterns, and in the perception of the plane of polarized light.

It is little more than 15 years ago that Professor v. Frisch astonished us by his announcement that bees could steer their way by the pattern of polarised light in the blue sky. But now we know that all insects can perceive the plane of polarisation of light; and the study of the fine structure of the retina of the compound eye with the electron microscope has come very near to demonstrating how it is done.

In the study of insect hearing, as in the other senses, the development of electronic methods of recording nervous disturbances in single cells and axons, has led to a rapid expansion of knowledge in recent years. The most intriguing problem about the hearing of insects was how they are able to recognise the insect songs which we find indistinguishable.

It turns out that although insects cannot discriminate pitch, as we can do, their ears have an exceedingly small "time constant"; they can easily separate sounds which follow one another at intervals of less than 1/100th of a second. They are therefore extremely sensitive to changes

in "frequency modulation", that is, in the frequency with which pulses of sound succeed one another—a type of music to which we are almost completely deaf.

Lastly smell. Since the insect is covered by a continuous layer of cuticle, it was problematical how the organs of smell, the tiny hairs on the antennae, could operate. Now we know, from studies with the electron microscope, that these little hairs are perforated by hundreds of minute pores in which the terminal dendrites of the sensory neurones are freely exposed to the atmosphere.

A large part of the study of insect physiology consists in repeating on the insect what has already been done on other animals. The ubiquity and uniformity of the basic processes of biochemistry, and the main elements in cellular structure, in all the living organisms on this planet are among the most significant biological discoveries of this century. The insects fall into this scheme, but they do show minor variants here and there.

At the time of the 1912 Congress, Gowland Hopkins had recently demonstrated the existence of essential "vitamins", and essential amino acids, necessary for the nutrition of mammals. The requirements of insects for both these groups of substances are remarkably similar to the needs of vertebrates. But my former colleague, the late R. P. Hobson, showed many years ago that for the insects cholesterol is in effect a vitamin. Carnitine and unsaturated lipids are other substances, essential for some insects, which mammals can manufacture for themselves.

There are many insects which feed on restricted diets, incomplete diets, or food devoid of micro-organisms. They cope with this situation by an intimate association with hereditary micro-organisms carried in special cells (the mycetocytes). These had been first described in ants and cockroaches by Blockmann in 1884 and later in Anobiids by Escherich in 1900. The symbiotic organisms are transmitted from one generation to the next in an amazing variety of ways—the unravelling of which will always be associated with the name of Professor Paul Buchner and his school in Munich.

These organisms were long believed to assist in digestion; but during the past thirty years their main significance has been proved to lie in the provision of those components, vitamins of the B group, certain essential amino acids, that are deficient in the diet. This has been proved in the blood-sucking insects, in insects feeding on plant juices, beetles in dry seeds, and most recently in the cockroaches. But the colonies of flagellates and bacteria, in the hindgut of termites and the larvae of Scarabaeid beetles, do play an important part in the digestion of cellulose for their hosts.

At the turn of the century, many different people had conceived the idea that the gonads of insects might influence the secondary sexual characters, as do the gonads of vertebrates. But all the experiments of excision or transplantation gave negative results, and thus the belief grew up that insects do not secrete hormones. It was not until 1917 that Kopeč carried out his simple but convincing experiments on *Lymantria* and showed that the brain is the source of a hormone which induced pupation in the full-grown caterpillar and continued development in the pupa. Experiments in other Lepidoptera raised doubts about this conclusion; for in them pupal development seemed to be controlled by a centre of some kind in the thorax.

It was not until the nineteen thirties that detailed studies of the hormonal control of moulting and metamorphosis were undertaken. As the result of these studies (which are still being actively continued in many parts of the world at the present time) we know that insects have a well-defined endocrine system which controls their growth, metamorphosis and reproduction.

The source of the hormone that induces growth and moulting is the gland of internal secretion named the "ventral gland" of the head, or the prothoracic or thoracic gland, according to its situation in different species. This gland is activated by a second hormone produced by neurosecretory cells in the dorsum of the brain and apparently discharged into the bloodstream from the corpus cardiacum. The "moulting hormone" (named "ecdyson") exists in a number of closely related chemical forms; it appears to be a steroid derived from cholesterol. The nature of the brain hormone is a subject of active study at the present time.

The moulting hormone may lead to larval moulting, to pupation, or to adult development. The course taken depends partly on the stage of development of the insect, but chiefly on the presence or absence of the secretion of the corpus allatum, the so-called "juvenile hormone".

If the juvenile hormone is present in sufficiently high concentration, the moulting larva develops into a larva again; if the hormone is absent it undergoes metamorphosis to the adult.

The chemical nature of the juvenile hormone is subject to debate at the present time. The isoprenoid alcohol "farnesol", which can be synthesised by insects, and can be extracted from them, will give precisely the same effects as the juvenile hormone if it is suitably formulated and administered. It looks as though the natural hormone is very closely related to substances of this type.

In the adult insect, another hormone from the neurosecretory cells, and the juvenile hormone from the corpus allatum, are responsible in varying degrees in different insects for the sexual maturation of both sexes.

But these are not the only processes that we now know to be controlled by hormones: colour change, diurnal rhythms of activity, diuresis, the rate of heart-beat, and the movements of other viscera, are all regulated by hormones, many of them derived from neurosecretory cells. Indeed the wheel has gone full circle; we seem to be returning to the views of the Ancients, which were supposedly discredited during the last century; more and more of the activities of the body seem to be regulated by humours from the brain. It is interesting to recall that the demonstration of hormone secretion by the neurosecretory cells in the dorsum of the insect brain was the first definite function for the neurosecretory cells to be proved in any animal.

One of the puzzles of insect physiology in 1912 was the performance of the flight muscles. The way in which the indirect muscles of flight deform the thorax and indirectly cause the wings to rise and fall, was well understood. It had been shown by Marey in the last century, by the use of the kymograph and by other means, that flies can beat their wings at a frequency of several hundred times a second. Subsequent studies in biochemistry and electron microscopy have shown that the flight muscles of insects differ very little in essentials from the muscles of vertebrates—but no vertebrate muscle will contract and relax at a rate exceeding about twenty to thirty times per second.

In fact, the indirect flight muscles of insects do not contract and relax in response to nervous stimuli. The thorax, with the wings articulated to it, undergoes a high-speed oscillatory movement which alternately stretches the indirect muscles and then releases them at a rapid rate. The course of this movement is determined by the structure of the thorax. The muscles must be kept in a state of activation by the nerves. What is peculiar about the insect flight muscle is that, provided it is kept activated in this way, it is caused instantly to contract when stretched and instantly to relax when released. Given the capacity to respond in this way there seems to be almost no limit to the speed at which the muscles can operate. The midge *Forcipomyia*, with its wings cut short, will vibrate them at the rate of more than 2000 times a second.

Apart from these interesting peculiarities, what has the study of insect physiology contributed to general biology? Fifty years ago the biochemical study of oxidation in the living body had only just begun. Much was done during the next ten years. Otto Warburg produced evidence for the existence of an enzyme which catalysed the combination of hydrogen with oxygen, the so-called "Atmungsferment"—but the nature of this agent remained undiscovered. In 1925, when David Keilin was studying the haemoglobin that is found in the larva of *Gasterophilus* he observed a series of absorption bands in insect muscles which he recognised as the bands of haematoporphyrin.

These bands had been seen many years before by McMunn who could never gain acceptance of his observations. But what Keilin saw was entirely new. He saw that in the flight muscles of the bee and of the wax moth, the pigments responsible were alternately oxidised and reduced within the living insect. He at once realised that here was the universal oxidising system that everyone had been looking for: the chain of cytochromes through which electrons were transferred to molecular oxygen so that this became "activated" and caused to unite with the hydrogen detached from the body fuels.

To-day everybody knows about cytochrome; but I suspect that there may be many biochemists who do not realise that the discovery of cytochrome was a product of the study of insect physiology.

My other example goes back to the middle thirties, when German, French and American workers were studying the eye-colour mutants of *Ephestia* and *Drosophila*. In both insects, the amino acid tryptophane was converted by a series of enzymes through kynurenine and oxy-kynurenine to the ommochrome pigments of the eye. The mutants "vermilion" and "cinnabar" resulted from defects in this metabolic chain. Each link in the chain was controlled by a specific enzyme which was the product of a specific gene.

This classic story was the first clear-cut example to support the "one gene, one enzyme" hypothesis. It provided the foundation for the *Neurospora* work that has since formed the main basis for this theory which is now generally accepted.

I hope you will agree that these are impressive examples of the potential contribution of insect physiology to general biology. But I believe that the great era of insect physiology is yet to come. As Crick has pointed out, anyone who sat down and thought at any time during the past fifty years could have inferred that inheritable characters must be enshrined or as we say nowadays "encoded" in some really stable molecule; and the nucleic acids were the only possible candidates. Now this is accepted, and the orderliness of development is seen as the result of the step-wise activation of particular components of the genetic code.

We have long realised that metamorphosis is a genetic switch or transformation of just this kind; the controlling factor being the presence or absence of the juvenile hormone. Environmentally directed polymorphism among the individuals of a species, and cellular differentiation within the tissues of the individual, are commonly regarded as comparable phenomena.

But these are largely general ideas and impressions. They must be given substance and detailed biochemical proof. There is certainly no more important problem in biology to-day; and I submit that there is no more promising medium than the insect, in which this problem can hopefully be studied.

FINAL PLENARY SESSION

SOME ASPECTS OF AUSTRALIAN ENTOMOLOGICAL RESEARCH

D. F. Waterhouse
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It is, indeed, an honour to address the 12th International Congress of Entomology at its closing session. I take this as a recognition of the vigorous and active—although still small—groups of entomologists that have come together in various centres on the Australian scene in the last 2 or 3 decades. I could not hope to provide in the time available an adequate picture of what each of the groups is doing, so I have selected several projects from the Commonwealth Scientific and Industrial Research Organisation's Division of Entomology to which I have belonged for a little more than quarter of a century. This Division has a responsibility to help solve the insect problems of Australia. The most effective solutions often require long-term, field and laboratory experiments and frequently a basic approach involving extensive taxonomic, physiological and ecological studies to serve as sound basis for action. Rather more than half of the Division's research programme deals with basic research of this kind and the remainder with more direct means of reducing pest numbers. From its establishment in the late 20's, when the Division was specially concerned with biological control, it has always been strongly oriented towards seeking ways of reducing the importance of pests by means other than the use of insecticides. For this reason our research activities have not been as greatly influenced as those of many other institutions by the post-war boom in insecticides nor, more recently, by the widespread preoccupation with pesticide hazards. We are, of course, concerned that insecticides should be used as safely and effectively as possible and have worked vigorously to this end, for, in line with the views expressed many times at this Congress, there is no doubt in our minds that insecticides will be a mainstay of insect control for as far as we can look into the future.

Rather than restricting my remarks to a single topic, I have chosen several of the many current projects in which the research group to which I belong is involved. To enable me to deal with a wide range of topics, I shall first of all show a film introducing some of the problems and then, later, take up several in more detail. In doing so I have chosen to deal rather more with the applications of the research than with the research itself, but I would like to emphasise at this stage, that the practical results have been underpinned by extensive basic research.

FILM—CURRENT RESEARCH IN THE DIVISION OF ENTOMOLOGY

As I have already indicated, the Division of Entomology has been heavily committed in its attack on pest problems to the ecological approach, which aims, essentially, at making full

use of such elements of pest control as exist in nature. Perhaps those that spring first to mind are parasites, predators and pathogens: their systematic propagation is what is commonly called *biological control.* Their systematic preservation from destruction by pesticides used at the same time has been called *integrated control.* I wish to talk about several of our attempts at what we have come to call *Pest Management.* Just as man manages the populations and environments of his domestic animals and cultivated plants for his maximum benefit, he can subject the population and environment of an insect pest or weed to manipulation in a variety of ways, adding up to a systematic attempt to turn the tables on it while still favouring beneficial species. Pest management may involve the strategic use of chemicals where the advantages of their use outweigh the disadvantages.

By a detailed study of the ecology (and especially of the population dynamics) of our most important pests, we are gradually developing the ability to "manage" them.

I shall mention three examples of our current work. Naturally some aspects of this work have followed, or proceeded simultaneously with, overseas developments: other aspects have developed quite independently.

Pome Fruit Pests

I am sure that you are all familiar with the pioneering work of Dr. Pickett and his colleagues on the integrated control of pests of apple orchards in Nova Scotia. Our studies, led by Dr. P. Geier, are aimed at understanding the ecology of orchard insects well enough to allow the management of Codling Moth and associated pests in Australia.

There are three important characteristics of Australian pome fruit orchards from the viewpoint of pest control:

(*i*) pome fruits are all introduced, without close relatives in the native flora;

(*ii*) they are grouped in discrete, widely separated and often isolated districts;

(*iii*) growing seasons are very long, particularly for apples (e.g. the Granny Smith blossoms in October and is harvested six months later).

The pests, too, have certain important characteristics, thus there are:

(*i*) fewer noxious species than in other growing areas (codling moth, exotic armored scales, exotic phytophagous mites, woolly aphis, oriental peach moth, pear slug, plus a few native species such as the light brown apple moth, *Epiphyas postvittana* a tortricid). Of these the most important is undoubtedly codling moth, the adults of which seldom disperse more than a few hundred yards.

(*ii*) very few effective natural enemies of major exotic pest species (e.g. there are no effective parasites of codling moth or oriental peach moth);

further

(*iii*) because of the long growing season, some pest species can build up to heavily damaging numbers. This is often aggravated by the lack of efficient natural enemies;

and

(*iv*) because of the isolation of some growing districts, many orchards are entirely free from certain major exotic pests (e.g. there is no codling moth in Western Australia, no San José scale in Tasmania, and no European red mite in most mainland districts).

The control procedures and their intensity vary considerably because of differences between local situations. On the whole, however, they have been distinguished since the War by repeated application of broad-spectrum insecticides.

This has had three major consequences:

(*a*) in the short term, it has allowed the immediate suppression of the damage;

(*b*) in the long run, it has induced insecticide resistance in some major pests (e.g. resistance to DDT in codling moth);

and

(*c*) caused the destruction of many parasitic and predatory species, and a subsequent upsurge in the rate of increase of several important pests (e.g. light brown apple moth, mites, woolly aphis and possibly scales).

Growers currently use 6 or more sprays of a broad spectrum organophosphorus or carbamate insecticide and achieve good control of codling moth. They are beginning to suffer, however—and progressively more heavily—from damage by our native light brown apple moth. This is widespread, attacks a very wide range of plants and is normally kept well below

economic numbers by a series of effective native enemies, both parasites and predators. With the development by light brown apple moth of resistance to all of the insecticides currently used for codling moth control and the simultaneous destruction of its native enemies by these same insecticides, serious and widespread outbreaks of light brown apple moth are occurring. It is clear that an adequate understanding of the population dynamics of the orchard fauna is required in order to plan effective measures.

Under Australian conditions the population which can be attained by codling moth in any one season depends largely upon the number that overwinter successfully. Studies show that most of those which succeed, spin up on the fruit trees, whereas most that leave the trees succumb to ants and other general predators. Measures which reduce or eliminate the satisfactory cocooning sites on a tree (such as pruning, scraping off loose bark, or filling up crevices with non-phytotoxic plastic) cause a dramatic reduction in the numbers which survive to produce the first spring generation. We have developed a new toxic mixture for bands for the tree trunks which may be used as a further measure for trapping and killing wandering larvae. Under experimental conditions these measures, combined with either 3 or, perhaps, 4 early season sprays with the highly-specific plant insecticide, Ryania, have given commercial control of codling moth. Because of the poor powers of dispersal of codling moth, local suppression of numbers gives good local control of this pest. Since Ryania has no effect on the natural enemies, it holds promise of dealing simultaneously with both the codling moth and light brown apple moth problems, because it permits natural enemies to deal effectively with the latter.

Grain Storage Pests

All countries face problems with insects attacking stored grain and many use insecticides or fumigants to reduce or eliminate damage. Australia is no exception and, in order to ensure freedom from insects, much of our export wheat is now protected by 8 ppm malathion—a level currently accepted by experts as being harmless to man.

Our recent studies, under Mr. S. W. Bailey, have been concerned with three methods which do not involve insecticides:

(*i*) Air-tight Storage. This has been used commercially in some countries, notably Argentina, since the war, but a number of the factors involved had not hitherto been investigated.

When grain is stored in air-tight containers any insects present soon die. The respiration of the insects and that of the grain itself, produces carbon dioxide at the expense of the oxygen initially present in the intergranular air: by the time less than ½lb grain per ton (i.e., 1 part in about 5,000) has been consumed, lethal conditions have been attained. The cause of death has been shown to be the depletion of oxygen—the accumulation of carbon dioxide being relatively unimportant. Death occurs when the oxygen has been reduced from its atmospheric value of 21% to about 3-4%. A fully instrumented, experimental, airtight silo is giving valuable information for planning the construction of new silos where grain—if necessary, of higher moisture content than normal—can be stored indefinitely without damage by insects. The advantage of this method is that, if effectively carried out, the emerging grain does not carry with it the nucleus of an infestation which will later build up to damaging populations.

(*ii*) Grain aeration. Because few if any of our existing silos can be made airtight with available techniques, an alternative means for avoiding damage to grain stored in them is required. It has been found in several countries, notably U.S.A., that, if sufficient cool air is available, this can be utilised in a simple ventilation system to reduce the temperature of the grain to a level at which the insects are unable to increase their numbers. We have collected data on the temperatures necessary to suppress reproduction in each species (a temperature of 55°F is desirable, although 60°F greatly lowers the reproductive rate). We have also developed a simple recording device to obtain data on air temperatures throughout the Australian wheat belt. This information is required to design appropriate machinery for each site. Already this method is being used in commercial practice in all Australian States.

(*iii*) Effect of physical disturbance. Insect pests can be killed by mechanical shock, but the forces required to kill larvae and pupae inside individual grains are great enough to cause an unacceptable amount of damage to the grain itself. It has been shown that the cause of the insects' death is rupture of the cuticle.

We now find that much smaller forces applied more frequently are effective in preventing the development of immature stages. Whereas some larvae survive impact forces as high as 150 feet per second when this is applied only once during the development period, none survives a force of 21 feet per second if this is applied daily, and only 4% survive this treatment if applied once weekly during the immature stages. Even dropping the grain only 9 inches, equivalent to a force of about 7 feet per second, causes a mortality of over 40% if done daily and of over 20% if carried out twice weekly.

These latter forces are so low that it seems unlikely that gross physical damage is the cause of death as it is a matter of common experience that animals of small mass can drop substantial distances without injury. Furthermore, if a treatment, which is lethal when spread out over the developmental period of the insect is given all at one time, a very much smaller mortality is caused. Thus, forces of 16·8 feet per second given twice daily (i.e. for each of 30 days) cause 99% mortality. The same total physical force applied as 30 treatments, one immediately after the other, causes a mortality of less than 40%. Current work is attempting to establish the cause of death. Attempts to stain neuro-secretory materials that might be released from the corpora cardiaca have not yet met with success, one hypothesis being that, whereas the occasional release of such materials under stress may be physiologically harmless, their repeated release may cause sufficient upset to normal metabolism as to be lethal. It is interesting that experiments conducted while the larvae are under CO_2 anaesthesia or chill coma have shown equal effectiveness. Another possibility is that, in some way, the lipid layer of the cuticle is irreversibly damaged by occasionally repeated impacts and that death is due to desiccation.

Direct observation of the effects of the treatment on the insects' behaviour and activity is impossible because they live within the wheat grains. An auditory method has now been developed by which a permanent record of the insects' feeding and movement activity during the development period may be made. It is hoped that, if the cause of death can be discovered, it may be possible to exploit it in some practical fashion.

Cattle Tick

For the third of my examples of pest management I shall return briefly to the cattle tick—where we have developed three alternatives to the graziers' usual practice of dipping all their animals in an acaricide every 4 to 6 weeks throughout the year. I might add that the cattle tick has developed, in turn, resistance to arsenic; D.D.T.; lindane, dieldrin and related compounds; many organophosphorus compounds (including dioxathion, diazinon, carbophenothion); and to the carbamate, carbaryl. There remain very few materials which can be used.

(*a*) Strategic dipping

One of the new methods simply involves the more effective use of acaricides and is called strategic dipping. This is the use of dippings at 3-week intervals so as to interrupt the tick life cycle for a period long enough to allow most of the free-living larvae in the pasture to die. Then follows a period when dipping is unnecessary and, when ticks reappear, a further group on dippings at 3-week intervals is carried out. Although about as many dippings may be required as with treatments at 4 to 6 week intervals, instead of tick infestations being high on the animals for most of the year, the tick numbers never need reach the level where the animals are harmed by the ticks.

(*b*) Pasture spelling

Where it is desired to avoid the use of insecticides as far as possible the second of the "new" methods may be used.

Studies of the survival of the non-parasitic stages of the cattle tick on pastures showed that most tick larvae did not survive nearly as long as formerly thought. This pointed the way to a practical tick control measure—by "spelling" or resting the pasture. Although destocking the land has long been used as a method for cleansing areas of ticks in eradication programmes in U.S.A. and N.S.W., the periods employed for eradication were, of necessity, very long because they were based on maximum known survival periods of larvae—plus a substantial safety margin. However, we found that a tremendous improvement in tick control could result from greatly reduced spelling periods because only very few of the ticks survived nearly as long as their most hardy fellows. Spelling pastures in central and northern Queensland for

3 months in the summer and $4\frac{1}{2}$ months in the winter resulted in a 75% reduction in the number of dippings and approximately the same reduction in the average tick burden. In Southern Queensland a 4-month rotation, strategically timed in relation to the seasonal history of the tick, enabled dipping to be dispensed with altogether.

(*c*) Resistance of cattle to ticks.

The third of the new approaches to cattle tick control involves the breeding of tick-resistant animals.

A few animals in almost every herd permit the development of only very few of the tick larvae attaching to them and we are studying the heritability and mechanism of the tick resistance of these cattle. The results indicate that the ability to prevent effective development of the cattle tick on their hide is indeed highly heritable and that it should be a comparatively simple matter to develop herds that have such a high degree of tick resistance that treatment with acaricides is only seldom necessary. If my optimism is justified the day is in sight when the Australian beef industry will be saved many millions of pounds loss each year. Furthermore we will not need to rely at all heavily on the use of insecticides.

Manipulation

If we are to make the best of Pest Management there must be a wide public awareness of the many and varied ways in which we can manipulate the populations of insect pests. Our artist has recently prepared an illustration on this theme for Rural Research, a publication which reaches most extension workers in Australia. The puppet strings in this illustration represent the deliberate manipulation of nature by man. Under the dark cloud in the background—the bad old days of Silent Spring and the indiscriminate use of insecticides—two aeroplanes blanketing the country with broad spectrum insecticides are barely seen. From the ten fingers, puppet strings lead to ten current activities. First a specific, male attractant lures the Queensland Fruit Fly to a poisoned bait; then the liberation of radiation-sterilized male fruit flies disorganises breeding; next, special toxic bands for the codling moth help to break its life cycle; then comes breeding for resistance to cattle ticks and pasture spelling to break the tick life cycle.

On the second hand, lethal radiation controls pests of stored grain; the predatory bdellid mite takes a heavy toll of the lucerne flea an important pasture pest; barriers produced by local application of insecticides to the soil successfully prevent attack of termites; *Sirex* larvae in pines are attacked by an introduced species of *Rhyssa*; and finally we have *Asolcus* the very promising parasite of green vegetable bug eggs which was seen in the film. Sometimes it is the selective use of insecticides, sometimes biological control, sometimes the use of resistant varieties and sometimes an alteration in management practice.

Tissue Culture

I propose to end my account where it started in the film, namely on insect tissue culture. As you have probably gathered, we are tremendously excited with its possibilities.

Blood

You will remember that the requirement for a small amount of heat-treated insect blood was mentioned. This strictly limits the growing of the cells to those laboratories which have facilities for obtaining adequate quantities of insect blood, and this is quite a problem. Attempts to adapt the *Antheraea* cells to a medium containing 1 to 5% calf serum, instead of insect blood, have now proved successful and cells have been growing well and dividing (about every 48 hours) for about 3 months. We are hopeful, therefore, that the cells will soon be readily available to any laboratory equipped for tissue culture.

Mosquito cells

Another development of great interest is the successful establishment by Dr. T. Grace of a strain of cells from the yellow fever mosquito *Aedes aegypti*. These cells have been subcultured now for about 12 months and should prove of value to workers in the field of medical entomology and virology.

Preservation

It is interesting that, as with mammalian cells, the insect cell lines can be deep frozen ($-125°F$) following addition of 10% glycerol to the medium and revived after a lengthy

period. For *Antheraea* periods up to 2 years have been tested with a 70 to 80% survival. With the mosquito cells comparable tests have only been running for 4 or 5 months.

Viruses

Plant, mammal and, of course, insect viruses are all known to multiply in insect cells. It is likely, therefore, that insect tissue cultures will enable many interesting problems relating to viruses to be examined. If, for example, poliomyelitis could be grown, this would greatly diminish the possibility that exists in monkey kidney slices that undesirable contaminating viruses might end up in the polio vaccine.

You have already seen a cell die from infection by a cytoplasmic polyhedral virus and the way in which living cells immediately recognise a dead one. Cytoplasmic polyhedral viruses are known only from the midgut of insects, yet this one grows excellently in cells derived from the ovarian sheath. An interesting fact is that it appeared spontaneously in a culture which was apparently healthy and normal for 10 months.

Two years ago another *Antheraea* virus appeared which completely prevents us from breeding this species anywhere in the vicinity of our Canberra laboratories. The virus particles closely resemble poliomyelitis. They are present in the nuclei of the gut epithelium. This virus belongs to a fairly uncommon group of insect viruses which are not occluded in polyhedra or granules.

A pasture scarab virus has also been successfully grown. This is *Sericesthis* Iridescent Virus, a close relative of *Tipula* Iridescent Virus, so called because the regular molecular arrangement within the abundant virus particles produces a bluish, iridescent colour. This virus can be grown in larvae of the wax moth *Galleria* and in the *Antheraea* tissue culture cells.

Many virus problems, such as latency can now be studied in these cells. Thus the *Antheraea* cells in culture are still, after 4 years, carrying this latent virus that can be triggered to produce a virulent virus at any time by appropriate means.

Insecticides

Tissue culture cells can also be used for the study of the effects of insecticides on strains from either resistant or susceptible insects. The few experiments carried out so far have been very interesting. When crystals of D.D.T. were introduced into a flask containing moth cells in culture, these cells were quite unaffected, even though they wandered over the D.D.T. in their amoeboid movements. When the medium was poured off, centrifuged to remove all D.D.T. crystals and diluted extensively, it killed mosquito larvae by virtue of the dissolved D.D.T. Is it typical then that many individual tissues of insects are insensitive to D.D.T. and what avenues for investigating the mode of action of D.D.T. does this open up? Clearly there are many exciting things which are waiting to be done with cultures of insect cells.

In conclusion, may I say that I hope that an opportunity will, before long, present itself to many here to-day to visit Australia to see what is going on and, perhaps, to become as intrigued as we are by the multitude of fascinating entomological problems which remain to be tackled.

LES EFFETS DE GROUPE ET LES ACTIONS PSYCHOSOMATIQUES CHEZ LES INSECTES

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Pendant longtemps, on a cru que les animaux vivant en société ne différaient des animaux solitaires que par une tendance à se grouper.

Des biologistes (Rabaud 1937 et autres) se sont même employés à démontrer qu'il en était bien ainsi.

Or l'animal social diffère du solitaire non seulement par les particularités de son comportement mais aussi par ses réactions à certaines stimulations périphériques émanant de son semblable.

On a établi avec rigueur qu'entre les Insectes sociaux règne une attraction mutuelle très forte qui détermine la formation du groupe et en assure le maintien et la stabilité.

L'existence de cette attraction mutuelle ou interattraction a été démontrée avec un grand luxe de détails chez les Blattides, les Abeilles et les Termites.

Les Blattes (*Blatella germanica*), dispersées au hasard dans une enceinte où les conditions sont les mêmes en tous les points, se groupent de telle façon que leur rassemblement ne peut s'expliquer par la simple probabilité. Nécessairement, des causes extrinsèques (et peut-être intrinsèques) interviennent et provoquent le groupement. L'expérience a démontré l'exactitude de l'hypothèse. L'attraction olfactive paraît être la cause dominante du groupement, les chimiorécepteurs siègeant sur les antennes (Ledoux 1945) reçoivent la stimulation.

Verron (1963) a analysé avec minutie l'attraction mutuelle chez les Termites à cou jaune (*Calotermes flavicollis*) ; il en a montré les variations selon les castes et les stades de développement. La substance attractive est l'hexène-3-ol-1 sous la forme cis. Si les antennes, les palpes labiaux et maxillaires, portent, semble-t-il, les chimio-récepteurs dont les informations déterminent l'attraction, Verron a pourtant observé que les Termites privés de ces appendices n'en continuent pas moins à manifester une interattraction peu diminuée. La fermeture des stigmates respiratoires, obtenue en introduisant les Termites dans une atmosphère d'oxygène, s'accompagne de l'abolition de l'attraction mutuelle. La tentation de conclure que certains chimiorécepteurs résident dans les troncs trachéens est grande.

Entre les Abeilles ouvrières règne une vive attraction. Ainsi quelquesc entaines d' ouvrières dispersées, après avoir été anesthésiées par l'anhydride carbonique, à leur réveil se groupent en une grappe unique, en moyenne au bout de deux heures. Il importe de noter que le nombre limite optimum pour la formation de la grappe est de 75 (50% de grappes) ; au-dessous, les ouvrières demeurent dispersées ou ne forment que de petits groupes comptant 3 ou 4 sujets (Lecomte 1949-1956) qui finissent par former la grappe.

Plus la masse d'ouvrières (les appelants) est grande, plus forte est l'attraction qui ne paraît pas être d'origine olfactive. Lecomte (1949) incline à croire que l'attraction sociale, dans le cas des Abeilles, est à base de stimulation auditive (réception de vibrations dont la fondamentale se situe aux environs de 30 Hz).

L'attraction qu'exerce si violemment la reine sur ses filles, les ouvrières, s'est avérée être de nature olfactive; l'acide céto-9 décène-2 transoïque, élaboré par les glandes mandibulaires de la reine, en est l'agent efficient.

Wilson (1962) estime avoir montré qu'une substance volatile, probablement l'anhydride carbonique, est responsable de l'attraction et du rassemblement des ouvrières de la Fourmi, *Solenopsis saevissima.*

Ainsi l'Insecte social est attiré par son semblable et cette attraction est mutuelle. Chaque individu fonctionne donc à la fois comme un stimulateur et comme un réacteur. C'est là le propre de la sociabilité. Tout groupement où cette condition ne se trouve pas réalisée n'appartient pas au domaine du social.

Dans le comportement social, comme dans presque tout comportement, deux composantes interviennent: à savoir, *A*, les réactions à des stimuli spécifiques émanant du congénère, *B*, la pulsion interne qui sensibilise l'organisme aux dits stimuli. A cette dernière, Wheeler (1926) donna le nom d'appétition sociale. Elle se met plus aisément en valeur chez les Vertébrés que chez les Insectes, mais ici nous n'avons pas à en traiter.

Les stimulations qu'exerce le compagnon social (ou mieux les compagnons sociaux) sur l'individu considéré isolément ne se bornent point à déclencher l'attraction mutuelle. Elles ont bien d'autres effets que nous allons examiner avec quelques détails.

Le groupe crée par lui-même un milieu particulier, qu'il soit social ou non: accumulation des excreta, consommation rapide des aliments disponibles, etc. . . Dans certains cas, le groupement a des effets plus subtils: Georges Bohn et Anna Drzewina (1920) ont montré les premiers que les animaux, sociaux ou non, réunis dans un milieu confiné (il s'agit surtout d'animaux aquatiques) acquièrent une résistance ou une fragilité qu'ils ne possédaient pas isolés. Citons en exemple, le cas des Planaires marines (*Convoluta* ou *Procerodes*) isolées, qui, rapidement détruites par l'eau de mer diluée, résistent beaucoup mieux à la dilution si elles sont groupées. Allee (1930) a montré que la libération, par les individus placés en milieu hypotonique, d'ions Ca protège ceux-ci contre l'hypotonie. Les substances particulières (antibiotiques) que certains Végétaux (des Phanérogames aux Champignons) et des Bactéries déversent dans le milieu extérieur inhibent le développement d'autres plantes ou d'autres microbes; elles conservent à l'espèce son "espace vital" et son milieu nutritif.

Ces effets protecteurs constituent ce que les auteurs français et, à leur suite, les auteurs américains ont nommé *effet de masse*. Les animaux groupés, qu'ils soient de moeurs solitaires ou sociales, lui sont soumis. Il s'agit avant tout, sinon exclusivement, d'une modification du milieu par la surpopulation qui influe directement ou indirectement sur les sujets rassemblés.

Il existe à côté de cet effet de masse, une action du groupement propre aux sociétés animales, à laquelle nous avons donné en 1943 le nom d'effet de groupe, terme qui prête peut-être à confusion et qui mériterait d'être changé. Cet effet ne dépend point d'une masse plus ou moins considérable d'individus et peut parfaitement se manifester lorsque seulement deux sujets se trouvent en présence l'un de l'autre, ceci indépendamment de tout changement du milieu.

La physiologie des Criquets migrateurs, étudiée par Chauvin (1941) a fourni un bel exemple d'effet de groupe. Le fait de grouper des larves solitaires de *Schistocerca gregaria* engage celles-ci dans la voie de la grégarisation. On obtient de la sorte des individus à peu près identiques aux migrateurs grégaires (larves et adultes) trouvés dans la nature.

Les *Schistocerca* groupés grandissent plus vite que les isolés, probablement parce qu'ils mangent davantage. Ils muent une fois de moins et de ce fait ont, dans l'oeil composé, une strie brune de moins que les solitaires (6 stries chez les grégaires, 7 chez les solitaires). Les larves solitaires affectent une teinte verte, les grégaires ont des couleurs variées où se mélangent le noir, le vert et le rose.

Ces variations impliquent des différences du métabolisme de l'Insecte en fonction de "l'état social". Les larves solitaires ne contiennent que des traces d'un pigment, découvert par Chauvin (1941) l'acridioxanthine, qui est un ommochrome (dont le pigment rouge des yeux de Drosophile est le type), alors que les grégaires en sont bien mieux dotés. Ce pigment paraît être d'origine alimentaire, sa plus ou moins grande abondance est liée probablement à la perméabilité de la paroi intestinale à son égard. On peut inférer que la perméabilité de l'intestin est modifiée par l'effet de groupe: influence nerveuse sur les cellules de l'épithélium. Chauvin (1943) par une méthode de colorimétrie est parvenu à doser l'acridioxanthine et à mesurer de la sorte l'effet de groupe; le Criquet contient d'autant plus de ce pigment qu'il est plus "grégarisé".

Un phénomène social, dans ce cas précis, se montre mesurable en soi, par le dosage d'une certaine substance.

Ainsi, le groupement produit sur les *Schistocerca* les modifications morphologiques et physiologiques englobées sous le terme de "grégarisation" par l'intermédiaire de *stimuli précis* et c'est ce caractère qui confère à l'effet de groupe son originalité.

Au laboratoire, pour transformer un solitaire en grégaire, il suffit de le faire vivre en groupe d'une façon constante ou intermittente.

Dans la nature, lorsque certaines conditions écologiques (surtout climatiques) favorisent la pullulation des Criquets, la densité devient telle que l'effet de groupe se produit, c'est-à-dire que les membres de la population se grégarisent.

A quoi tient donc cet effet de groupe? Comme on peut l'obtenir avec une paire d'individus, on ne peut songer à l'influence du milieu modifié par la population.

Des larves de *Schistocerca* solitaires appartenant au premier stade groupées dans une enceinte obscure se grégarisent. On a montré que l'effet de groupe ne se manifeste que si l'animal conserve au moins un compagnon social dans son champ perceptif sensoriel; mais un individu placé parmi les autres et enfermé dans une cagette grillagée demeure solitaire.

Cette même larve placée à la lumière et dans une cagette à parois transparentes (verre) se grégarise.

Deux sortes de réceptions sensorielles jouent conjointement: les tactiles (tact général) et les visuelles. Pour la transformation des derniers stades de solitaires en grégaires ce sont surtout exclusivement les stimulations tactiles qui interviennent. L'ablation des antennes arrête ou ralentit considérablement la transformation du solitaire en grégaire.

Naturellement, d'autres stimulations ne peuvent être exclues. Ainsi, Loher (1960) a montré que sur les téguments de *Schistocerca gregaria*, mâles adultes, se sublimise une substance qui accélère la maturité sexuelle des jeunes mâles.

L'effet de groupe a toujours pour point de départ des stimulations sensorielles d'une nature particulière.

Il a été observé dans un grand nombre d'espèces d'Insectes. Nous retiendrons seulement les exemples les plus remarquables.

Les études de Faure (1943 *a* et *b*) sur les Noctuelles (Noctuae) *Laphygma exigua* et *Laphygma exempta* dont les chenilles se déplacent par troupes en rangs serrés manifestent un net effet de groupe qui assombrit la livrée des chenilles, passant du vert pâle-jaunâtre au gris foncé voire très foncé tandis que la tête devient noire. Les autres modifications éventuelles n'ont pas été recherchées. Il est possible que cet effet de groupe s'accompagne de phases dont la grégaire serait liée à l'accomplissement de migrations, mais les études faites jusqu'ici ne permettent pas de porter un jugement ferme sur ce problème. Les recherches de Faure sur *Spodoptera abyssinica*, Noctuelle commune en Afrique australe, donnent les mêmes résultats que celles menées sur les espèces sus-citées.

Les chenilles de *Pieris brassicae* vivent en société pendant leurs 2 premiers stades, ensuite le groupe se subdivise et finalement se dissout. Il semble que les réceptions tactiles assurent le maintien du groupe; le tissage d'un fil de soie marquant exactement la piste suivie par l'Insecte, au cours des jeunes stades, contribue à stabiliser la société, car les chenilles utilisent les fils de soie comme des conducteurs olfactifs (Long 1955).

Les chenilles de Noctuelles (*Plusia gamma*, *Prodenia litura* (Long 1953, 1955; Long et Zaher 1958, 1960; Zaher et Long 1959) ont donné des résultats analogues. Groupées, elles se développent plus vite que les solitaires, pèsent moins (larves et pupes) et sont plus petites. Les papillons eux mêmes sont de taille moindre. Les chenilles groupées se mélanisent plus ou moins fortement.

La teneur en anhydride carbonique n'intervient pas dans le changement de couleur, alors que les contacts paraissent exercer une forte influence sur la pigmentation des chenilles de la Noctuelle gamma (*Plusia gamma*). Il s'agit d'un incontestable effet de groupe puisque 50 pour 100 de la variation de couleur obtenue en groupant 81 Noctuelles s'observe sur deux chenilles mises en présence l'une de l'autre (Long 1955).

Sur le Lépidoptère *Exaereta ulmi*, Sharov (1953) a observé des faits analogues et a même parlé de phases liées aux vies grégaire ou solitaire.

Tous les Lépidoptères ne réagissent pas de la même manière au groupement. Ainsi, les Vers à soie ne manifestent un effet de groupe qu'après leur 4^{e} mue; il est alors important et consiste en une augmentation du poids individuel: au moment de la montée, pour un groupe de 250 vers, le poids est en moyenne de 4, 5g par individu, pour un groupe de 10 de 3, 5g, et pour les isolés de 2, 7g! (Legay et Pascal 1951).

La vie en société produit aussi des modifications morphologiques d'une grande amplitude sur les individus; pour le moment, laissons de côté la formation des castes dans les sociétés hautement organisées et intégrées et considérons les sociétés simples où l'interattraction paraît être le principal agent de la création et du maintien du groupe.

Les *Psyllipsocus ramburi* (Badonnel 1948), espèce exclusivement parthénogénétique, n'acquièrent d'ailes que s'ils vivent groupés. Les ailes apparaissent sur *tous* les individus dès que le groupe compte 4 individus et que chaque individu dispose d'un volume réduit à0, 3 cc, volume que Badonnel considère comme représentant le *seuil d'efficacité absolue* du groupement.

Les réceptions visuelles n'interviennent pas; il semble qu'on puisse attribuer l'effet à quelque stimulation chimique (Badonnel 1949). Le fait que les *Psyllipsocus* maintenus à une température supérieure à 23°C, bien que groupés, n'acquièrent plus d'ailes tient peut-être au simple fait qu'aux températures élevées, le métabolisme s'altère et ne permet plus, malgré l'effet de groupe, la formation des ailes. Ce cas, l'un des plus intéressants qui soient, appelle de nouvelles investigations.

Certains Pucerons (Hémiptères Aphididés) se comportent à l'instar des Psoques. Par exemple, Bonnemaison (1949, 1953) a établi que les Pucerons du chou (*Brevicoryne brassicae*) ne donnent des ailés que s'ils sont groupés. Le seul groupement des larves ne suffit pas à déterminer l'apparition d'ailés; il faut que leurs mères (virginipares aptères) soient aussi maintenues groupées.

Les Gryllides ont donné lieu à des recherches d'autant plus intéressantes qu'elles sont plus précises. En 1958, Chauvin montrait que le groupement accélère la croissance pondérale des Grillons domestiques (*Gryllulus domesticus*); l'effet se manifeste par la cohabitation, dans un même tube à essai, de deux individus quel qu'en soit le sexe. Mais seules les larves issues de femelles âgées sont sensibles au groupement; alors que la progéniture des jeunes femelles s'y montre insensible.

Chauvin a fort bien su séparer l'effet de groupe de celui du surpeuplement qui ralentit la croissance. L'effet de groupe a pour origine une stimulation sensorielle perçue par les antennes et les cerques. L'amputation de ces appendices supprime complètement l'effet de groupe.

Dans une longue série de publications, Madame Fuzeau-Braesch a étudié avec le plus grand soin l'effet de groupe chez *Gryllus bimaculatus*. La coloration de cet Insecte résulte du mélange de deux ommochromes (une xanthommatine et une ommine) avec un pigment de nature ptérinique contenus dans l'hypoderme; en outre, la cuticule renferme un pigment noir ou jaune dont la tyrosine est le précurseur ou l'un des précurseurs. Le groupement provoque un éclaircissement de la livrée de *Gryllus bimaculatus*. Dans le groupe réduit à deux sujets, la modification de la coloration s'observe, mais est moins forte que si le groupe est plus nombreux. Le stade auquel apparaît le changement de couleur paraît variable, mais n'est jamais antérieur à la sixième mue. L'étude de la variabilité génétique de couleur a permis d'affirmer qu'elle ne se confond pas avec l'effet de groupe; l'effet de groupe renforce la dépigmentation et s'ajoute à l'action des gènes qui la règlent. Même lorsque la sélection a augmenté la teinte sombre des sujets, l'effet de groupe en diminue l'importance.

Les recherches de Madame Fuzeau-Braesch ont donc levé une objection que l'on avait faite à l'interprétation de l'effet de groupe, en lui opposant que certaines variations de couleur ne dépendaient pas de lui, mais de facteurs génétiques. Elles ont rendu à chaque cause la part qui lui revient.

Cet auteur a écrit en termes excellents "Les sélections opérées déplacent les répartitions des génotypes et jouent sur un caractère de nature quantitative; le groupement et l'isolement viennent modifier les réalisations des phénotypes en déterminant le *niveau* auquel s'effectue le virage pigmentaire".

Dans les Grillons à polymorphisme alaire (*Gryllus argentinus, G. scapripedus, G. marginatus*), l'isolement favorise le brachyptérisme, et le groupement, le macroptérisme.

Le comportement des Grillons se modifie sous l'influence du groupe; l'agressivité diminue ou disparaît, tandis que les mâles élevés dans l'isolement témoignent d'une extrême agressivité à l'égard des congénères de leur sexe. Les sujets appartenant à un groupe tiennent les pattes postérieures relevées, les tarses ne touchant plus le substrat, les deux premières paires de pattes assurent à elles seules la sustentation de l'Insecte. Il va de soi qu'une telle posture modifie dans une certaine mesure les réceptions cinesthésiques du sujet.

Lévita (1964) a montré expérimentalement que l'effet de groupe chez *Gryllus bimaculatus* dépend surtout d'une stimulation tactile, perçue par les antennes et d'une stimulation visuelle. Le Grillon isolé dans une enceinte dont les parois sont des miroirs présente les principales modifications propres à l'effet de groupe. La suppression de réceptions visuelles et tactiles diminue l'effet de groupe mais ne l'abolit pas entièrement; ce résultat laisse entendre que d'autres stimuli, olfactifs ou vibratoires, contribuent à réaliser l'effet de groupe. Selon Mlle Lévita les sensilles siègeant sur les cerques de *Gryllus bimaculatus*, contrairement à ceux de

Gryllulus domesticus, ne jouent aucun rôle dans l'effet de groupe. Ainsi, le déterminisme de ce phénomène varierait d'une espèce à une autre.

Notre information sur le mécanisme même de l'effet de groupe demeure très pauvre. Les meilleurs documents ont été fournis par P. et L. Joly (1949, 1951, 1953, 1959). Ces auteurs greffent à des *Locusta migratoria*, élevées en groupe dense et présentant la plupart des caractères de la phase grégaire, des corpora allata prélevés sur des *Locusta* du même type. Cette opération a pour effet de faire apparaître sur les sujets receveurs une coloration verte caractéristique des Criquets de la phase solitaire. Ainsi, les glandes endocrines excitées par les centres cérébraux réagissent en plus ou en moins et modifient de la sorte l'anatomie et les fonctions de l'individu.

Dans les sociétés d'Insectes hautement organisées, l'effet de groupe existe avec une force bien plus grande que dans les sociétés plus simples; toutefois, il devient plus difficile d'en discerner la nature.

Rappelons que les résultats obtenus par les sociétés de Termites rendues artificiellement homogènes ont largement contribué à établir la notion d'effet de groupe. Un groupe de 50 nymphes de Termites à cou jaune (*Calotermes flavicollis*), très sensiblement du même âge et peu éloignées de leur dernière mue, celle qui les transforme en imagos ailés, au bout de quelques semaines, les uns suivent leur destinée normale, acquérant yeux composés et ailes, tandis que les autres, après une mue, deviennent des sexués de type néoténique, ou, perdant leurs attributs particuliers, forment une sorte d'individus, les *pseudergates*, à aspect de larves qui, demeurent longtemps sous cette forme ou par la suite, grâce, à de nouvelles mues, deviendront soldats, voire sexués, (Grassé et Noirot 1945). Autrement dit, au bout d'un temps plus ou moins long, la société homogène acquiert une composition hétérogène, avec les castes propres à l'espèce et selon des proportions quasi normales.

L'individu, du fait même de la composition de la société, évolue dans un sens particulier. A s'en tenir aux apparences, on peut écrire que le groupe détermine la destinée et la caste de l'individu. De nombreuses expériences ont confirmé le fait.

L'action du groupe est indéniable, mais il convient d'en préciser la nature. Des travaux effectués sur les Abeilles permettent d'entrevoir non pas une mais plusieurs solutions.

Indépendamment, Butler et ses collaborateurs (1959-60) en Angleterre, Mlle Pain et Barbier (1960) en France, ont montré que les substances sécrétées par les glandes mandibulaires de la reine (*queen substance*)exercent une action considérable sur la physiologie et le comportement des ouvrières. L'une de ces substances, l'acide céto-9 décène—2 transoïque, inhibe la construction des cellules royales; associée à une autre substance elle acquiert d'autres propriétés, elle exerce une vive attraction sur les ouvrières, dont elle inhibe, en outre, l'ovogenèse et stimule la construction des cellules d'ouvrières. Cette deuxième substance, non encore précisément définie, donne, après méthylation par le diazométhane, de l'acide phénylpropionique et de l'acide phénylacétique.

Les ouvrières, le fait est bien connu, nourrissent leur reine et, de ce fait, entretiennent avec elle d'incessants contacts. Elles la lèchent et absorbent sans doute le liquide sécrété par les glandes mandibulaires.

Ce ne serait donc pas une stimulation sensorielle qui agirait sur les membres de la société mais des substances chimiques ingérées par chacun d'eux, en quantité infime sans doute, mais suffisante pour modifier leurs fonctions et leur comportement. A de telles substances, on a donné les noms d'ectohormones (Bethe, 1932) et de sociohormones (Grassé, 1948). Comme les substances en question ne tirent pas leur origine d'une glande endocrine, le terme d'hormone est inadéquat. Un terme nouveau, mais mal fait, a été proposé c'est celui de phéromone (Karlson, 1960).

On peut imaginer, sans que la preuve expérimentale irréfutable en soit fournie, que chez les Termites, les effets observés dans l'expérience relatée plus haut sont dus à l'absorption de quelques substances prises sur les sexués que les ouvrières lèchent avec une inlassable avidité. Si une telle hypothèse est exacte, et selon nous elle est fondée, elle paraît, au moins sous sa forme simplifiée actuelle, non susceptible d'expliquer la différenciation des soldats et des pseudergates.

Il reste beaucoup à apprendre sur le rôle que jouent les échanges alimentaires ou trophallaxie dans la biologie des Insectes sociaux. On sait par l'utilisation des substances radioactives

incorporées aux aliments que les matières ingérées passent avec une surprenante rapidité dans un grand nombre sinon dans la totalité des membres de la société.

Il n'est d'ailleurs pas dans nos intentions de discuter ici le déterminisme des castes chez les Isoptères. Mais, nous discernons dès maintenant que sous le terme général d'effet de groupe, on désigne un ensemble de phénomènes dont la réalité est certaine mais dont les causes sont fort variées.

On doit distinguer au moins deux modes d'action du groupe sur l'individu: 1° par l'ingestion de phéromones, 2° par la stimulation sensorielle.

Il est vraisemblable que, dans les deux cas, les mécanismes ne sont pas radicalement différents. On peut imaginer que les phéromones influent soit directement sur les glandes endocrines, soit par l'intermédiaire du système nerveux; la stimulation sensorielle atteint d'abord les centres supérieurs qui, excités, agissent ensuite sur les glandes endocrines.

L'ingestion de phéromone ne peut avoir d'importance qu'au sein de sociétés où la trophallaxie est de pratique courante et où le léchage assure une "communication chimique" directe entre les individus. Dans les autres sociétés, la stimulation sensorielle demeure l'agent efficient de l'effet de groupe et, pour en marquer le caractère propre, nous qualifierons son action *d'effet psychosocial.*

Il nous paraît évident que l'effet de groupe à point de départ sensoriel ou *effet psychosocial* entre dans le vaste ensemble des phénomènes psychosomatiques. L'existence de ceux-ci chez les Insectes solitaires est une certitude. V. Labeyrie (1960) en a fourni deux très beaux exemples. L'Hyménoptère ichneumonide *Diadromus* sp. parasite de la Teigne du poireau (*Acrolepia assectella*) a une fécondité qui dépend étroitement des rapports qu'il entretient avec son hôte. Expliquons nous. Si, chaque jour, la femelle dispose d'une chrysalide de Teigne, sa fécondité demeure stable, mais si on lui en offre cinq la production des oeufs est multipliée par 1,33. La réduction du temps de présence des hôtes, c'est-à-dire des chrysalides, abaisse l'activité ovarienne et le nombre des oeufs pondus. La diminution peut atteindre la moitié de la quantité moyenne.

Le toucher par les antennes du cocon qui enveloppe la chrysalide paraît être le stimulus agissant sur l'ovaire, en passant, bien entendu, par les centres nerveux et les glandes endocrines. L'amputation des antennes exerce sur les ovaires le même effet que la suppression de l'hôte. Si on propose à la femelle de *Diadromus* des cocons vides, on stimule efficacement les ovaires mais les oeufs ne sont pas émis, car le contact de la tarière avec la chrysalide est seul capable de déclencher le réflexe de la ponte. Les oeufs non pondus sont résorbés dans les ovaires mêmes.

La fécondité de la Bruche des Haricots (*Acanthoscelides obtectus*) dépend largement de la présence de grains dans la sphère sensorielle de la femelle. En même temps, la production des oeufs s'accroit significativement et la résorption d'ovocytes intraovariens diminue.

On découvre que les Insectes pourvus, nous le savons, d'un riche assortiment de récepteurs sensoriels répondent par de profondes modifications physiologiques aux messages qu'ils reçoivent de l'extérieur.

Vus sous cet angle, bien des phénomènes demeurés jusqu'ici inexpliqués deviennent intelligibles.

Une fois de plus, on constate que l'Insecte présente, sous une forme qui lui appartient en propre, des phénomènes que l'on croyait réservés aux seuls Vertébrés. Ce dont nous sommes également sûrs, c'est qu'un nouveau champ d'investigation s'ouvre à la curiosité de l'entomologiste.

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RESOLUTIONS AND ANNOUNCEMENTS SUBMITTED BY THE PERMANENT COMMITTEE

1. Resolution from Section 1. (Systematics, including Phylogeny)

Whereas, priority, beginning with Jan. 1, 1758, is the basic principle of entomological nomenclature as it is of zoological nomenclature in general; and

Whereas, the International Commission on Zoological Nomenclature has Plenary Powers to suspend the application of the International Code of Zoological Nomenclature for the purposes of promoting stability and universality, or of avoiding serious confusion; and

Whereas, these Plenary Powers suffice for the truly serious cases of confusion or of long usage of biologically important names; and

Whereas the new Code contains "escape clauses", such as those concerned with family names, that are aimed at promoting stability in various aspects of nomenclature without either application of Article 23b (the so-called 50-year rule) or use of the Plenary Powers; but

Whereas, Article 23b, the Limitation on the Law of Priority, is considered to have serious weaknesses and in its present form to be objectionable and unnecessary to entomology, and even actually detrimental to it, to a degree that could not be remedied by any mere interpretive declaration;

Therefore, be it resolved that the XIIth International Congress of Entomology directs the Permanent Committee of the International Congresses of Entomology to propose and strongly recommend to the International Commission on Zoological Nomenclature that the field of entomology, in the broad sense, be exempted from the provisions of paragraph b of Article 23 of the International Code of Zoological Nomenclature. For the purposes of this resolution, entomology in the broad sense is defined as the study of Hexapoda, Arachnida, and Myriapoda.

2. Resolution from Section 9a. (Agricultural Entomology).

Profound environmental changes caused by the present expansion of productive land use lead to a drastic reconstruction of local insect fauna on newly developing areas, resulting in elimination of many species and rapid increase in populations of those which adapt to the new conditions and become outstanding crop pests.

We request the Permanent Committee of Congress to draw the attention of all authorities connected with large scale planning of land use (notably I.U.B.S., F.A.O., U.N.E.S.C.O.) to the hazards from the local insect fauna which represent a vast reservoir of potential pests and to the need for:

(1) inclusion of insect surveys in the general surveys of the areas selected for a particular type of development.

(2) studies on populations of species acquiring pest status, particularly in the tropics and subtropics where comparatively little is known about the dynamics of pests and where pest problems will be specially serious.

3. Location of next Congress

An invitation to hold the next International Congress in Moscow in 1968 was received from Prof. G. J. Bey-Bienko, Vice-President of the Entomological Society of the U.S.S.R. The Committee recommended that this be accepted.

4. Retirements and Appointments to the Permanent Committee

Mr. N. D. Riley, President of the Permanent Committee, has expressed his wish to resign and the Committee regretfully accepts his resignation. The resignation of Mr. W. R. Thompson has also been accepted.

The Committee has been fortunate enough to be able to nominate Dr. S. L. Tuxen as President in place of Mr. Riley.

The Permanent Committee proposes to the Meeting the election of the following to the Committee:

Dr. P. Freeman (United Kingdom)
Dr. G. P. Holland (Canada)
Dr. V. Landa (Czechoslovakia).

5. Honorary Member of Congresses

It was proposed that Mr. Riley be appointed an Honorary Member of Congresses in view of his long association with them and his service to entomology in general.

The foregoing resolutions, recommendations and proposals, submitted by the Permanent Committee were approved by Congress.

VOTE OF THANKS TO LONDON ORGANISERS

Mr. Chairman, Ladies and Gentlemen, It is an honour and great pleasure for me to have the opportunity to try to express the feelings of the overseas members of the present Congress. All of us have been Congress members indeed and, it seems to me, that at the same time we have shared the feeling of being welcome guests of our British entomological colleagues.

During these days of contacts between entomologists from all over the world we have had opportunities to discuss many urgent problems of our multifacetted science with colleagues working in other countries, using various methods, studying often the same problems from quite different view-points and often drawing controversial conclusions too . . .

These discussions were always fruitful and friendly, they showed that nowadays entomologists of various specialities have reached success in the consolidation of their efforts and approaches to the study of insects—those enemies and friends of mankind.

Our discussions took place not only during the Congress meetings held simultaneously in conference-rooms from A to N (not yet to Z!) but also in all corridors and lounges, in streets and buses, in bars and gardens—everywhere.

Our hosts contributed to the contacts of colleagues enabling "effet de groupes", according to the terminology of Professor P.-P. Grassé, when organising numerous excursions, official and informal receptions, spontaneous symposia, etc.

All has always been interesting and spiritual—especially when combined with tasting various spirits!

All of us enjoyed wonderful, typically British, organisation of the present Congress, the exact realisation of everything planned.

No reproach can be addressed to the Organisers. Both the overseas visitors and the

British colleagues know to whom we are obliged to for the successful activity of this splendid Congress. The Organising Committee, general organisers and especially our Chairman, Professor O. W. Richards and the Secretary-General, Doctor Paul Freeman, our hosts, have had many hard days performing the giant work of directing the present Congress which has been full of marvellous days.

Being engaged in the study of soil insects, I know what a great labour is done by hidden living species. I am sure that there are many colleagues whose hidden work contributed to the success of the Congress.

I am sure that I express the unanimous feeling when addressing the words of our sincere gratitude, of our hearty thanks to the Organising Committee, to Professor Richards and Doctor Freeman and to other organisers of our fruitful and pleasant Twelfth International Congress of Entomology.

C'est le sentiment des touts les participants du Congrès—notre gratitude respectueuse aux organisateurs du Congrès, notre grand merci!

Im Namen aller Kongressmitglieder möchte ich den Organisatoren des Kongresses unseren herzlichen Dank aussprechen!

Taking into account that the next, Thirteenth Congress of Entomology will be held in Moscow, in the capital of the U.S.S.R. and of Soviet Russia I would like to add in Russian—Bolshoye spasibo!

M. Ghilarov

BENEFACTORS AND ACKNOWLEDGMENTS

The subscription was fixed at £8 and it soon became clear that there would be a gap between the estimated expenditure and the expected receipts from membership fees. An appeal for funds was therefore circulated to interested bodies and it is with much pleasure that the Organising Committee records its thanks to the following for their support:

Donations of £50 or more—Boots Pure Drug Co. Ltd.; Messrs. Cooper McDougall & Robertson Ltd.; Cyanamid International Corporation; Dow Agrochemicals Ltd.; Fison's Pest Control Ltd.; International Council of Scientific Unions; Imperial Chemical Industries Ltd.; Leeds Philosophical Society; Murphy Chemical Company Ltd.; Rentokil Research Laboratories; Royal Entomological Society of London; Royal Society of London; "Shell" Research Ltd.

Donations were also received from—Birmingham Natural History Society; Messrs. Cuprinol Ltd.; Lancashire and Cheshire Entomological Society; C. W. Mackworth-Praed, Esq.; Northumberland Natural History Society; Pan Britannica Industries Ltd.; Pyrethrum Bureau; Messrs. Richardson & Starling Ltd.; Sorex (London) Ltd.; Universal Crop Protection Ltd.

The Officers and Organising Committee of the Congress wish to express their thanks to:—

The Rector and Governing Body of the Imperial College for the use of lecture rooms and other extensive facilities;

The President and Council of the Imperial College Students' Union for the use of the Students' Union;

Her Majesty's Government for the Reception for overseas members held at Lancaster House;

The Trustees and Director of the British Museum (*Natural History*) for the use of the Lecture Hall for film programmes, for allowing the Museum to be used for the Reception on the opening evening and for setting up an exhibit of books from the Library;

The Governors and Director of the Commonwealth Institute for allowing their galleries to be used for the Reception on the final evening;

The Vice-Chancellor of the University of London for the evening Reception at Senate House;

The Hon. Miriam Rothschild for the Reception at Elsfield Manor;

Shell Research Ltd. for the evening Reception and film show;

Royal Photographic Society and *British Broadcasting Corporation* for their special exhibits.

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SECTION 1.—SYSTEMATICS (INCLUDING PHYLOGENY)

The following papers were read but the authors did not wish for publication in these Proceedings:

Leston, D. (U.K.). Tracheal shifts in the wings of Heteroptera.

Micks, D. W. (U.S.A.). Biochemical differentiation of intraspecific strains of mosquitoes.

Townes, H. (U.S.A.). Some parallel modifications in mandibles and ovipositors of the Ichneumonidae (Hymenoptera).

Ehrlich, P. R. (U.S.A.). The broader implications of numerical taxonomy.

WING-VENATION IN RELATION TO PHYLOGENY

THE PERIODS OF ORIGIN AND DIVERSIFICATION OF THE SUPERFAMILIES OF THE HOMOPTERA-AUCHENORRYNCHA AS DETERMINED BY A STUDY OF THE WINGS OF PALAEOZOIC AND MESOZOIC FOSSILS

J. W. Evans

Australian Museum, Sydney

There is, at present, lack of agreement in respect to several relationships claimed between fossil Homoptera and present-day superfamilies. In order to help resolve this problem an analysis has been made of the venation, venational trends and some associated features of the forewings, or tegmina, of Recent Homoptera, and the results have been used in assessing the affinities of some Palaeozoic and Mesozoic fossils.

If a comparison is made between the venation of the tegmen of the Recent relict cicada, *Tettigarcta crinita* Distant and that of the Permian fossil, *Prosbole reducta* Martynov, no venational differences will be observed, and the only significant factor in which the two tegmina differ from each other is in the position of the transverse nodal line in relation to the proximal branching of *M*. This correspondence in venation demonstrates the stability of this structural feature within the Homoptera.

A great diversity of venational types occur within the Cicadelloidea. Nevertheless, it is possible to recognize five principal basic patterns, each of which is associated with a particular family. Among the venational features shared in common by these families is the invariable separation of *M* into two principal branches proximally and the division of *Cu* into *Cu1 a* and *Cu1 b*. With the exception of the Membracidae, another common feature is the basal incorporation of *M* and *R* into a single vein.

Similar venational features occur in the tegmina of certain Upper Permian and Upper Triassic Homoptera.

The venation of the tegmina of Recent cercopoids differs from that of cicadelloids in the presence of a short *Sc*; a frequently greater development of *R1*; the invariable presence of *Rs*, and by the reduction, usually to a single vein of *M*. Furthermore, *M* is either basally incorporated in the same vein as *Cu1* or else it may be joined to *Cu1* by a proximal cross vein. In those tegmina in which *M* is branched, the proximal division takes place distally of the branching of *Cu1*.

Another differentiating factor between the tegmina of cicadelloids and cercopoids is in respect to their texture. The surface of the tegmina of most cicadelloids is smooth, although a few are punctate. The tegmina of cercopoids, on the other hand, although sometimes smooth are more usually coarsely punctate, or, rugose.

The venation of the Fulgoroidea presents a special problem and while in general, it is usually possible to recognize the tegmina of fossil fulgoroids as such, this cannot always be done.

If illustrations of the tegmina of Permian and Triassic Homoptera are examined with the factors described above in mind it will be found that apart from anomalous forms and, those with a nodal line (which may be regarded as cicadoids), that the majority of the remainder would seem to have belonged to the Cercopoidea and not as had previously been presumed, anyhow by the present author, to the Cicadelloidea.

The Cicadoidea and the Cercopoidea are in general, structurally stable groups and this stability suggests that evolutionary equilibrium was achieved well before the commencement of the Tertiary.

The Cicadelloidea, on the other hand, are far from stable. Not only do many of their structural characteristics occur at different levels of evolutionary development in the various comprised groups and several intertribal sequences may be recognized, but it would seem that a number of tribes and subfamilies has been differentiated comparatively recently, that is to say during, or even since, mid-Mesozoic times.

It is accordingly suggested that during Permian, Triassic and early Jurassic times the Cercopoidea and Cicadoidea were undergoing considerable evolutionary divergence and that,

at that time, many diverse groups became differentiated. Some of these, such as the Dysmorphoptilidae and the Ipsviciidae in the Cercopoidea, and the Palaeontinidae in the Cicadoidea, will have become extinct by the commencement of, or during, the Cretaceous. Others, which survived into the Cretaceous will by then have reached a degree of comparative stability which has subsequently been maintained.

It is assumed, on the other hand, that during Permian and Triassic times, the Cicadelloidea, which may have represented an unimportant part of the Homopterous faunas of the times were comparatively inactive from the evolutionary point of view and that it was not until the Jurassic that they received an evolutionary impetus which resulted in the proliferation of the numerous and diverse present-day subfamilies and tribes.

Such a hypothesis, as well as explaining the present comparative evolutionary stability of the Cercopoidea and the Cicadoidea, would account also for the retention in some of the Cicadelloidea of various generalised features, which are no longer found in representatives of the other groups.

The suggested early-acquired stability of the Cercopoidea and the Cicadoidea may possibly be correlated with the fact that the nymphs of both groups, unlike those of the Cicadelloidea and Fulgoroidea, live in a specialised environment. On the other hand, the late evolutionary radiation of the Cicadelloidea may have an association with adaptive opportunities provided by the change from a gymnosperm to a predominantly angiosperm flora, which took place in mid-Mesozoic times.

So far as the Fulgoroidea are concerned, while they have great stability in cephalic characteristics, the existence of no less than twenty separate families implies a period of former evolutionary diversification. While, it is presumed that this will have been well before the commencement of the Tertiary it is not known whether it will have preceded the Jurassic.

Earlier, attention was drawn to the fact that the venation of cicadoids has not changed in essential features since Permian times. Subsequently, it has been shown how, within the several, and diverse families, of the Cicadelloidea, the position of initial branching of *M* in respect to the branching of *Cu1*, has remained identical in all families. Because of this established stability of venation it is claimed that clues to relationships based on venation, though sometimes liable to misinterpretation, are nevertheless more dependable by themselves, than evidence made available by any of the other morphological features of fossil insects.

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EVIDENCE FOR TRACHEAL CAPTURE IN EARLY HETEROPTERA

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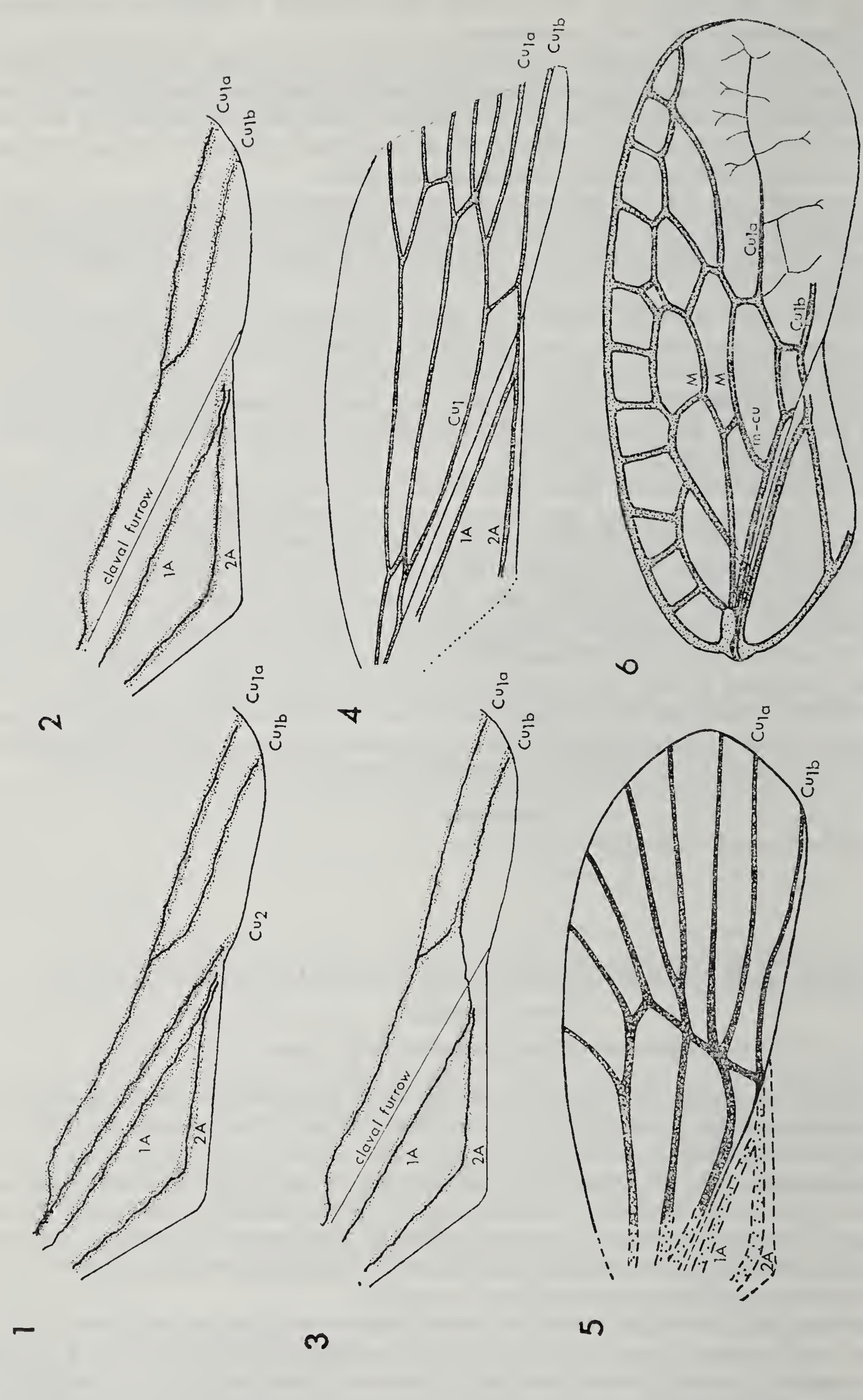
Leston (1962) has shown that tracheal capture, where the trachea of one vein comes to lie in the lacuna of another, is widespread in the Heteroptera, occurring both as individual variation and as an established condition.

One example, where the trachea of *1A* in the forewing crosses the claval furrow to lie in a distal remigial vein, occurs in all three divisions, and probably arose once only, early in the group's history. The extinct family Actinoscytinidae (U. Permian to U. Jurassic) indicates how the situation probably arose, and also establishes the identity of the single cubitus in the heteropteran forewing, variously interpreted as Cu_1 and Cu_2.

In all actinoscytinid forewings where the clavus is preserved, the two anal veins form a Y-vein, whose apex crosses the claval furrow into the remigium of the wing in a typical heteropteran manner. In early forms, like the U. Permian *Actinoscytina*, and many specimens from the L. Trias of Kirgisia (fig. 4.), the cubitus shows the sinuous form typical of Cu_1 in Homoptera. Distally it is joined to the remigial extension of the anal Y-vein by an oblique vein. It is suggested that this vein is derived from the base of a second branch of Cu_1, and that the anal extension is formed largely from the distal part of the same branch.



FIGS. 1-6. Wings of Heteroptera. (1-3) hypothetical stages in the evolution of the cubito-anal region of Heteroptera; (4) un-named actinoscytinid forewing, L. Trias, Kirgisia; (5) *Microscytinella radians* Wootton, U. Trias, Australia; partly reconstructed forewing; (6) *Peloridium hammoniorum* Breddin, macropterous forewing, redrawn after China, with altered labelling.

The line behind Cu_1 appears much thinner than the adjacent veins, and probably represents the claval furrow only. Cu_2, which lies along the furrow in most Homoptera, was presumably already lost.

Figures 1-3 show three hypothetical stages in the evolution of the actinoscytinid cubito-anal region from an unknown ancestral form. In the latter (fig. 1) it is supposed that Cu_1 had two branches, that Cu_2 was present and tracheate, and that the anal tracheae were confined to the clavus. Cu_2 was subsequently lost (fig. 2); and the trachea of *1A* crossed the claval furrow and came to lie in the lacuna of Cu_1b, whose own trachea was reduced (fig. 3). The L. Triassic wing (fig. 4) is believed to show the last stage, except that a new vein has arisen around the tracheal bridge between *1A* and Cu_1b, and the latter is distorted into alignment with *1A*.

Later forms (fig. 5) show transverse alignment of several distal veins, including, when present, the base of Cu_1b, which thus appears as a cross-vein. A cross-vein occurs in this position in many modern Heteroptera, and Tanaka (1926) shows it to be sometimes supplied by a branch of the trachea of *Cu*, as postulated in fig. 3.

Peloridiidae (fig. 6), now usually classed as Homoptera, seem to show the same cubito-anal configuration as Heteroptera, and it is suggested that there too Cu_2 is lost, and the trachea of *1A* has been captured by Cu_1b. If it is assumed that the process occurred once only, this implies that the peloridiid and heteropteran lines had a common origin from auchenorrhynchous Homoptera.

EINIGE ALLGEMEINE GESICHTSPUNKTE FÜR DIE PHYLOGENETISCHE DEUTUNG DES FLÜGELGEÄDERS DER DIPTEREN

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Will man das Flügelgeäder zur Feststellung phylogenetischer Verwandtschaftsbeziehungen heranziehen, dann genügt es, ebenso wie bei anderen Merkmalen, nicht, einfach Übereinstimmungen oder Ähnlichkeiten festzustellen.

Man muß vielmehr scharf unterscheiden, ob die Übereinstimmung ursprüngliche oder abgeleitete Merkmale betrifft. Bei Übereinstimmung in abgeleiteten Merkmalen muß man sich noch fragen, ob Konvergenz vorliegt, oder nicht.

Konvergenz ist im Flügelgeäder der Dipteren außerordentlich häufig. Darauf achtet man aber allgemein, so daß es kaum notwendig ist, auf die Gefahren hinzuweisen, die sich aus den Erscheinungen der Konvergenz ergeben.

Weniger beachtet und daher gefährlicher ist die Erscheinung der Rückentwicklung, das sekundäre Wiederauftreten scheinbar ursprünglicher Merkmale. Eines der bekanntesten sogenannten Gesetze der phylogenetischen Entwicklung ist das Dollosche Irreversibilitätsgesetz. Weil dieses Gesetz so allgemein bekannt ist, scheut man sich offenbar bewußt oder unbewußt vor der Annahme, daß scheinbar ursprüngliche Merkmalszustände durch "Rückentwicklung" aus abgeleiteteren Zuständen entstanden sind.

Es scheint mir daher wichtig, auf eine Reihe von Situationen hinzuweisen, die im Flügelgeäder der Dipteren für eine Rückentwicklung, auf ein Wiederauftreten scheinbar ursprünglicher Merkmale sprechen. Es kann sich dabei um ein scheinbares oder tatsächliches Wiedererscheinen reduzierter Adern handeln. Der Verdacht, daß eine Rückentwicklung vorliegt, ist immer dann gegeben, wenn scheinbar sehr ursprüngliche Merkmale bei einer Gruppe auftreten, die erwiesenermaßen im System bzw. im Stammbaum eine sehr untergeordnete Stellung einnimmt.

Beispiel: G. H. Hardy (2) hat seiner Reticulation Theory of Venation vor allem die Nemestrinidae zugrundegelegt. Nach dieser Theorie soll ein netzförmiges Geäder den Ausgangszustand darstellen. Durch die Rückbildung von Adern sollen die einfacheren Geäderformen entstanden sein. Aber die Nemestrinidae sind zweifellos ein so untergeordneter Zweig im Stammbaum der Dipteren, daß es zu sehr großen Schwierigkeiten führen würde, wenn man das Flügelgeäder aller anderen Dipteren von diesem Zustande ableiten und

annehmen wollte, daß allein die Nemestrinidae den ursprünglichen Zustand bewahrt haben. Bequaert und Carpenter haben schon 1936 eine funktionelle Erklärung für die Entstehung der überzähligen Queradern gegeben. Die akzessorischen Queradern sind nach diesen Autoren bei den Nemestrinidae mindestens zweimal unabhängig entstanden. Demnach ist das netzförmige Geäder der Nemestrinidae bei den Dipteren als abgeleitetes und nicht ein ursprüngliches Merkmal, obwohl es dem Augenschein nach einem ursprünglichen Insektengeäder ähnlich sein mag.

Ein 2. interessantes Beispiel hat Nowakowski (5) bei einer Agromyzide, *Phytomyza aquilegiae*, beschrieben. Hier ist der vordere Ast des Radialsektors manchmal gegabelt. Bei allen anderen Cyclorrhaphen, selbstverständlich mit Einschluß der Agromyzidae, ist dieser Ast nicht gegabelt. Dasselbe gilt darüber hinaus für fast alle rezenten und fossilen Brachycera mit Ausnahme ganz weniger ursprünglicher Formen, von denen es noch nicht einmal sicher ist, ob sie wirklich Ausnahmen darstellen. Nun sind die Agromyzidae zweifellos ein so untergeordneter Zweig im Stammbaum der Brachycera, daß man nicht annehmen darf, hier allein sei die Gabelung des vorderen Astes des Radialsektors erhalten geblieben. Außerdem kommt diese Gabelung ja nur als individuelle Variante innerhalb der Art *Phytomyza aquilegiae* vor. Nowakowski ist daher sicher im Recht, wenn er annimmt, daß die Gabelung des 1. Astes des Radialsektors bei *Phytomyza aquilegiae* kein ursprüngliches Merkmal, sondern sekundär aufgetreten ist.

Die Frage nach der ursprünglichen Ausbildung des Radialsektors bei den Brachycera ist unter Umständen von großer Bedeutung für die Deutung fossiler Formen und damit zugleich für die Bestimmung des Alters verschiedener Teilgruppen der Brachycera. Ich habe (3) angenommen, daß bei den Vorfahren der Brachycera R_3 gemeinsam mit R_4 mündete und dann verloren ging. Die Tatsache, daß eine tatsächliche Verbindung zwischen R_2 und R_4 nur bei wenigen nicht nahe miteinander verwandten rezenten Formen vorhanden ist, legt die Vermutung nahe, daß diese Verbindung auch hier kein ursprüngliches Merkmal ist, sondern sekundär aufgetreten ist, vielleicht als Reaktivierung eines alten Faltenbettes von R_3. Aus diesem Grunde halte ich es noch nicht für erwiesen, daß die Gabelung des vorderen Astes des Radialsektors bei Lampromyia namaquaensis Stuckenberg (6) wirklich ein ursprüngliches Merkmal ist. Bei allen anderen Arten der Gattung ist der Ast einfach wie praktisch bei allen anderen Brachycera.

Oft kann die Frage, ob ein Merkmal des Flügelgeäders ursprünglich oder abgeleitet ist, entschieden werden, wenn man die Flügelform der betreffenden Gruppe im Hinblick auf eine spezielle funktionelle Bedeutung hin berücksichtigt. Dorthin gehört schon die oben erwähnte Deutung, die Bequaert und Carpenter dem netzförmigen Geäder der Nemestrinidae gegeben haben.

Besonders häufig hängen Veränderungen des Geäders mit einer Verbreiterung des Flügels, namentlich der Flügelbasis, zusammen:

Wahrscheinlich ist der Verlauf der Analadern bei den Fanniinae durch eine Verbreiterung des Analfeldes zu erklären. Dadurch entstand die eigenartige Krümmung im Verlauf der 2. Analader und das Heranrücken der 1. Analader an die 2. Die 1. Analader wurde verkürzt, weil die Endabschnitte beider Adern nicht mehr nebeneinander Platz hatten. Vielleicht hängt auch der Verlauf der Subcosta mit der Verbreiterung der Flügelbasis zusammen.

Es liegt nahe, die eigentümliche Dreieckform des Flügels mit den Paarungsflügen der Männchen in Verbindung zu bringen. Auch die Merkmale des Geäders würden dann letzten Endes dadurch bedingt sein. Allerdings sind sie auch bei den Weibchen vorhanden, die an den Paarungsflügen nicht teilnehmen und breitere Flügel haben. Hier könnte man annehmen, daß die beschriebenen Merkmale bei den Männchen entstanden und sekundär auf die Weibchen übertragen wurden. Es gibt ja Beispiele genug dafür, daß Merkmale, die in einem Geschlecht entstanden sind, auf das andere übertragen werden, obwohl sie hier keine funktionelle Bedeutung haben. Ich habe dieses etwas abgelegene Beispiel angeführt, um zu zeigen, wie viele Dinge man unter Umständen bei der Deutung des Geäders berücksichtigen muß.

Bei anderen Dipteren können durch die Verbreiterung des Flügels verschmolzene Adern sekundär wieder getrennt werden. Die sogenannte 1. Analader der Cyclorrhapha ist ein Verschmelzungsprodukt aus zwei verschiedenen Längsadern, die bei Orthorrhapha noch

getrennt sind. Es liegt daher nahe, diejenigen Flügel der Cyclorrhapha als ursprünglich anzusehen bei denen der Vereinigungspunkt der beiden Adern besonders nahe am Flügelrande liegt. Ich habe aber 1954 die Annahme zu begründen versucht, daß durch eine Verbreiterung des Analfeldes bei den Ortalidiformes eine sekundäre Aufspaltung der komplexen Ader erfolgen kann. Dadurch entsteht ein eigenartiger Zipfel an der Analzelle. Durch erneute Verschmälerung der Flügelbasis kann dieser Vorgang wieder rückgängig gemacht werden.

Für den Grundplan des Dipterenflügels habe ich 1954 die Annahme gemacht, daß der vordere Ast der Cubitalader mit dem letzten Ast der Media verschmolzen ist. Nun hat Möhn (4) einen Gallmückenflügel beschrieben (*Xenasphondylia*), bei dem vor der Cubitalisgabel eine Längsader vorhanden ist. Möhn bezweifelt die von mir angenommene Verschmelzung der Adern Cu_{1a} und M_4 im Grundplan des Flügelgeäders der Dipteren, weil die beiden Arten bei *Xenasphondylia* scheinbar getrennt erhalten sind.

Aber die Gallmücken sind ein sehr untergeordneter Zweig im Stammbaum der Dipteren, und die Asphondyliinae sind ein sehr untergeordneter Zweig im Stammbaum der Gallmücken. Es ist daher höchst unwahrscheinlich, daß gerade hier ursprüngliche Merkmale des Geäders erhalten geblieben sein sollen als bei allen anderen Dipteren. Wenn es sich hier nicht einfach um einen Rest von M_{1+2} handelt, dann ist es viel wahrscheinlicher, daß eine Trennung von M_4 und Cu_{1a} *sekundär* durch eine Verbreiterung des Flügels erfolgt ist. Wie mir Dr. Möhn bestätigte, unterscheiden sich die beiden Geschlechter von *Xenasphondylia* in der Breite der Flügel und die fragliche Ader ist nur bei den breiteren Flügeln vorhanden.

Ursprüngliche Verhältnisse im Geäder können auch dadurch vorgetäuscht werden, daß eine Ader an die Stelle einer verschwundenen anderen Ader tritt:

Der Basalabschnitt der Media ist nur bei wenigen Fungivoriformia erhalten. Bei den meisten ist er verblasst. Durch eine Verschiebung der Gabelstelle des Cubitus in Richtung nach der Flügelbasis kommt es aber dann zu einer Schrägstellung des Basalabschnittes von M_4 (tb), der in die Stellung des verlorengegangenen Basalabschnittes von M einrückt. Die weitere Entwicklung führt dann dazu, daß der vordere Ast der Cubitalisgabel seine ursprüngliche Verbindung mit dem hinteren Ast verliert und eine neue Verbindung weiter distal gewinnt. Solchen Flügeln kann man es nicht ansehen, daß der scheinbare Basalabschnitt von M in Wirklichkeit der schräg gestellte Basalabschnitt von M_4 ist. Trotz ihrer scheinbaren Ursprünglichkeit teilen solche Flügel mit den meisten Fungivoriformia das abgeleitete Merkmal des Fehlens des Basalabschnittes von M. Was als solcher erscheint, ist der an seine Stelle gerückte Basalabschnitt von M_4 (3).

Es wird oft gesagt, daß beim Vergleich verschiedener Flügel die Feststellung von Homologien Voraussetzung ist. Remane hat für die Feststellung von Homologien mehrere Kriterien angeführt, unter denen das "Kriterium der Lage" eine besondere Rolle spielt. Das zuletzt genannte Beispiel zeigt, daß dieses Kriterium manchmal sehr unzuverläßig ist. Aber auch dann, wenn bei sehr ähnlichen Flügeln alle einzelnen Elemente des Geäders tatsächlich homolog sind, genügt es nicht, daraus auf nahe phylogenetische Verwandtschaft zu schließen. Es ist vielmehr notwendig, sich in jedem Falle die Frage vorzulegen, wie die Übereinstimmung entstanden ist.

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VERÄNDERUNGEN DES FLÜGELGEÄDERS BEI TANYPODINEN (DIPTERA CHIRONOMIDAE) IM VERLAUF DER EVOLUTION

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Die Tanypodinen stellen innerhalb der Chironomiden eine in den einzelnen Entwicklungsstadien morphologisch gut abgegrenzte Unterfamilie dar. Im Imaginalstadium zeigt ihr Flügel einen bei Chironomiden sonst nicht auftretenden Verlauf des Radiussektor: R_{2+3} gabelt sich distal, R_2 geht in R_1 über und R_3 legt sich an C.

Aufgrund umfassender Untersuchungen der Tanypodinen darf man annehmen, daß ihre Stammform, der plesiomorphe Typ, relativ groß war und der Flügel entsprechend Raum zur Ausbildung der Adern bot. Im Verlauf der Evolution hat dann innerhalb dieser Unterfamilie ein Trend zur Verkleinerung der Arten eingesetzt. Offensichtlich brachte diese Verkleinerung den Larven und Puppen einen physiologischen und ökologischen Leistungsvorteil (1). Bei der Imago treten mit dem Kleinerwerden funktionsmechanisch bedingte Veränderungen an den Beinen und an den Antennengliedern, sowie bei verschiedenen Organen auf. Besonders deutlich treten sie beim Flügel in Erscheinung: C wird verkürzt, R_3 berührt nicht mehr C, R_2 und schließlich R_{2+3} verschwinden. Die Queradern *rm* und *mcu* verlagern sich proximal. Schließlich bildet sich ein Flügeltyp aus, der dem der Podonominen entspricht.

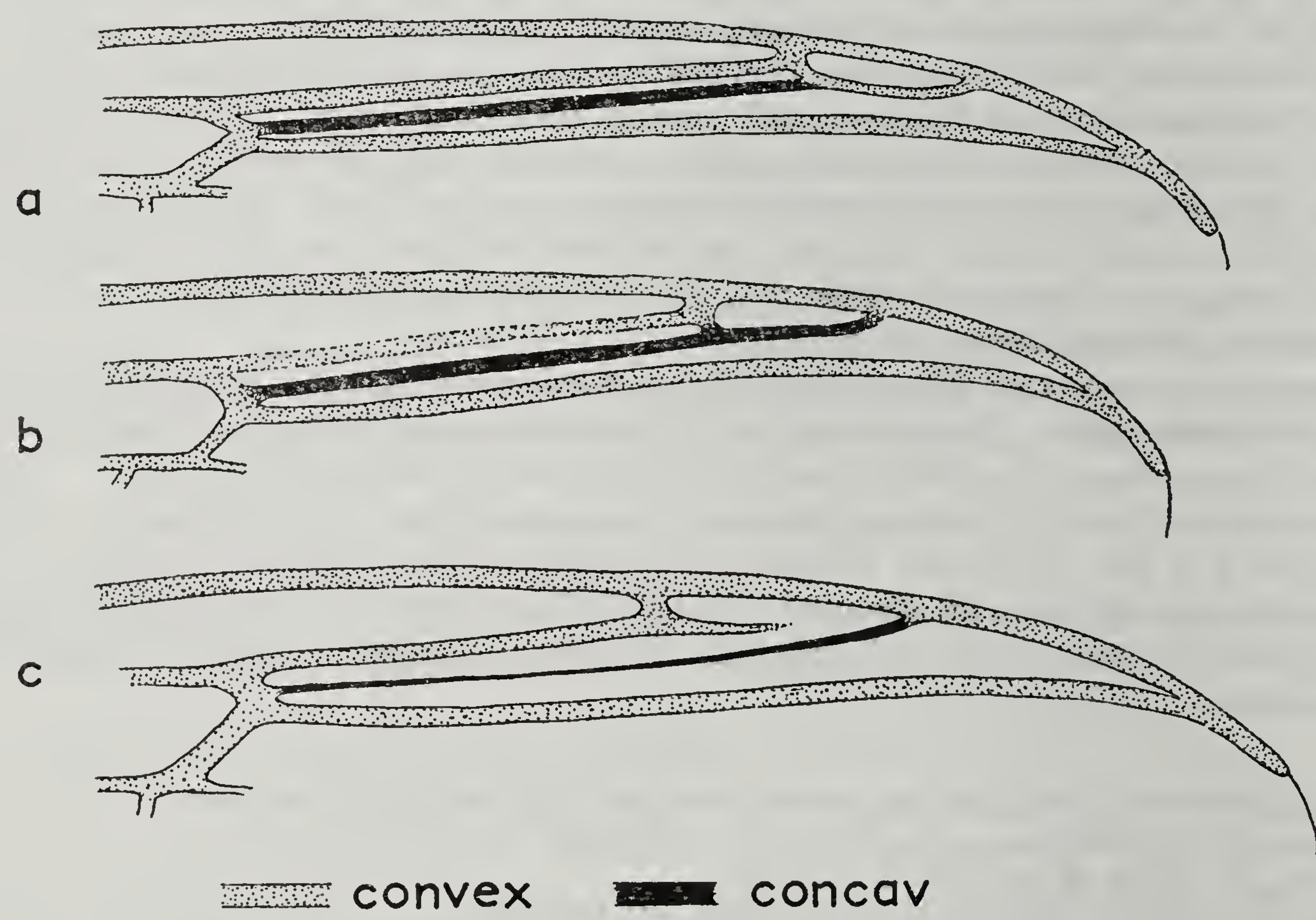

Abb. 1. Der Verlauf des Radiussektor bei verschiedenen Tanypodinen: (*a*) *Tanypus vilipennis;* (*b*) *Tanypus kraatzi;* (*c*) *Clinotanypus nervosus.*

Verschiedene Merkmalsbildungen sprechen dafür, daß die Podonominen sich schon bedeutend früher als die Tanypodinen von der Chironomiden-Stammform gelöst haben. Schon bei der Herausbildung der Ausgangsform der Podonominen dürfte aber ein ähnlicher Trend zur Verkleinerung der Arten wirksam gewesen sein, wie wir ihn heute noch bei Tanypodinen verfolgen können und der hier schließlich auch zum Verlust von R_{2+3} geführt hat. Die bekannten Podonominen sind im allgemeinen sehr klein.

Nicht befriedigend war bisher die Deutung der Radialadern beim Tanypodinen-Flügel. Eine neue und überzeugende Vorstellung von der Entwicklung des R_{2+3} bzw. R_2 und R_3 hat Lindeberg kürzlich gewonnen. Er griff die Beobachtungen auf, die Pagast am Flügel von *Diamesa cinerella* gemacht hatte. Bei dieser Orthocladiine ist R_1 stark verlängert. Noch vor ihrem distalen Ende zeigt sie die Tendenz mit C an einer Stelle zu verschmelzen. Bei anderen, und zwar nur großen Arten der Gattung *Diamesa*, die als besonders plesiomorph gilt, kann man das gleiche Bestreben feststellen. Diese Beobachtung zwingt zu der Annahme, daß bei der schon aus anderen Gründen groß geforderten Ausgangsform der Tanypodinen die Tendenz bestand, R_1 ebenfalls zu verlängern, zu verstärken und an C in dieser Weise anzulegen. Es widerspricht nicht den Befunden, an anderen Insektenflügeln, daß im Falle der Tanypodinen-Stammform R_1 vor seinem Ende mit C verschmolzen gewesen sein kann. Durch seine sekundäre Verlängerung ist R_1 mit R_{2+3} zusammengestoßen und hat sich, durch diese Ader verstärkt, von C distal der ersten Verbindungsstelle abheben können.

Nach der Deutung von Lindeberg sind R_2 und R_3 die Verlängerung von R_1, R_{2+3} gleich R_2 und R_{4+5} gleich R_3. Den stärksten Beweis dafür, daß R_{2+3} die Verlängerung von R_1 sei, sieht Lindeberg darin, daß R_{2+3} bei dem von ihm beobachteten Procladius-Flügel eine convex-Ader im Gegensatz zu R_2 und R_3 ist. Wie sich aber zeigt, ist bei einem großen Teil von Tanypodinen R_1 distal der Vereinigung mit R_2 im Sinne von Lindeberg eine concav-Ader wie R_2. Dennoch spricht viel für die Richtigkeit der Auffassung von Lindeberg. Ursprünglich ist die Verlängerung von R_1 eine convex-Ader. Dort aber, wo R_1 schwach ausgebildet ist und R_2 sich verstärkt, wird das Ende von R_1 in entgegengesetzter Weise von R_2 beeinflußt. (Abb.). Der betreffende Abschnitt distal der Verbindung von R_1 mit C—der alten Auffassung nach R_2—ist stets eine convex-Ader. Ganz deutlich wird die Ableitung von R_1 und R_2 innerhalb der Gattungen *Clinotanypus* und *Coelotanypus*. Hier hat sich R_1 sekundär verkürzt und von R_2 gelöst. Distal der ersten Verbindungsstelle mit C ist von R_1 nur noch ein kurzes convex-Aderende übrig geblieben, während R_2 ungestört bis zu C verläuft, wie bei einem Orthocladiinen-Flügel. Zu ähnlichen Bildungen ist es auch im Laufe der Evolution bei anderen Tanypodinengattungen, insbesondere bei Pentaneurini gekommen.

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VEIN VARIATIONS IN *PLAGIOLEPIS* (HYM. FORM.) AND THEIR POSSIBLE PHYLOGENETIC SIGNIFICANCE

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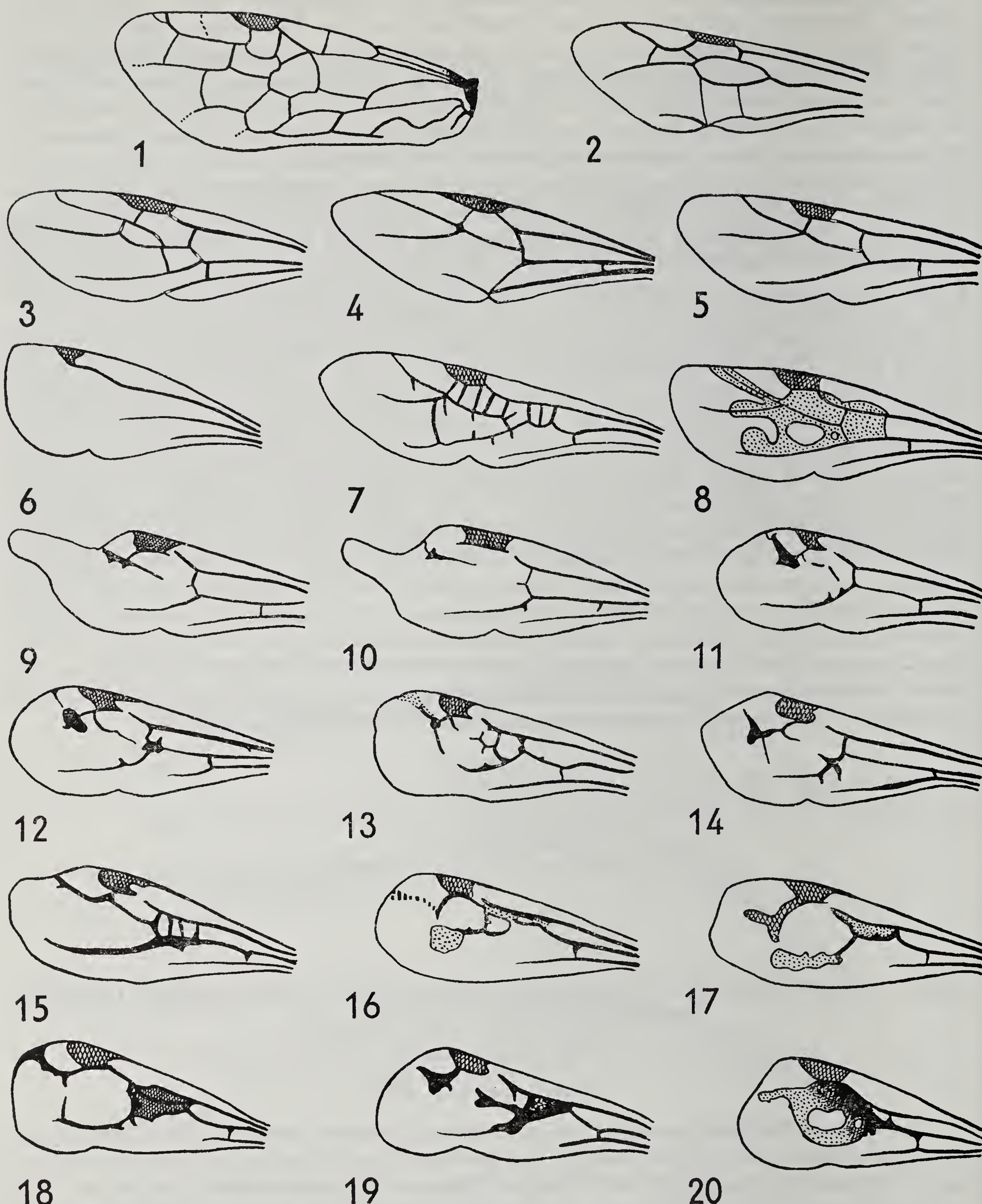
A colony of *Plagiolepis pallescens* For. ssp. *ancyrensis* Santschi collected in the Coastal plain of Israel containing only workers and winged females, showed conspicuous variations in shape and venation of the forewing in all 37 females. Most of the wings showed a reduction in the radial area (figs. 9, 10) or in the entire distal part of the wing (figs. 11-20). Variation occurred in three directions: (a) *reduction* of the distal part of *Cu* and crossveins, so that in a combined picture of all reductions only three longitudinal veins remained (fig. 6); (b) *addition of supernumerary veins*, chiefly crossveins between *sc-m* and *m-b*. A combined picture of all additional veins observed is given in fig. 7. In this way several closed *cu*-cells instead of one and 1-2 discal cells instead of the one normally open, are formed; a peculiar pattern of cross veins also occurred in the *cu*- and $d+sm_2$ cells; (c) *chitinization* of entire wing areas, of which a combined picture is given in fig. 8.

Although no direct evidence is available, the high correlation between types of variation of right and left wings in the same specimen suggests these variations are genetically controlled (figs. 9 and 10, 11 and 12, 16 and 17).



FIGS. 1-20. Wings of Hymenoptera. (1) *Pamphilius;* (2) *Eciton;* (3) *Ponera;* (4) *Camponotus;* (5) normal venation of *Plagiolepis;* (6)-(20) aberrations of *Plagiolepis.*

Vein reduction in the course of evolution in Hymenoptera is a well known fact, the primitive groups having the largest number of closed cells (fig. 1). Among the Formicoidea the primitive Dorylidae (fig. 2) and Poneridae (fig. 3) have a closed cu_2 and d, while in the Formicidae (Sf. Camponotinae) only cu_1 remains and d is open (figs. 4, 5). In many groups, e.g. Scoliidae, Sphecidae, Pompilidae, Apoidea the presence of 1-2-3 *cu* or 1-2 *d* cells are of value as generic or subgeneric characters. Reduction of vein pattern is often correlated with wing size, smaller wings requiring fewer cross veins than larger ones. Among the Camponotinae the large (17mm) forewing of *Camponotus* (fig. 4) shows a closed sm_1, in comparison with the small (3·5mm) wing of *Plagiolepis* (fig. 5).

Additional venation is restricted to cross veins (fig. 7); they occur chiefly in the *m*, *cu* and $d+sm$ cells, but never along the costal margin (*ic*, *r*). Besides veins which give rise to closed or almost closed cu_2 and $d+sm_2$ (figs. 12, 13, 14, 17, 18) a peculiar ladder-like cross vein pattern is observed in cu_1m (figs. 13, 15) and to a lesser degree in sm_1 and $d+sm_2$ (fig. 14). A closed cu_2 or cu_3 and the occurrence of two recurrent nerves is common in Hymenoptera, but large numbers of cross veins in *m* is unknown in this group. It is necessary to go to hemimetabolic orders, e.g. Plecoptera or Embioptera, for comparison, where we find analogous additional cross veins sometimes associated with brachypterism.

In many cases flow of chitin from the veins may be observed, forming chitinous patches (figs. 8, 16-20). If *Sc* and *Cu* adhere in the pupal wing pad, *Cu* is bent dorsally towards *Sc* (figs. 16-19) and the area around the point of connection may become heavily chitinized. Other diffuse chitinizations may occur at the distal part of the shortened *R* (figs. 13, 17), *Cu* (figs. 16, 17) and the additional 1st recurrent nerve (fig. 20). Analogous pronounced broadened veins are again found in brachypterous males of Trichoptera, Plecoptera and in the "nodal furrow" of the triassic rhynchotan *Dunstania.*

Looking for an explanation for the occurrence of these vein variations it is suggested that it is caused by probably one gene with pleiotropic effects, causing a weakening of the vein walls and so enabling an outflow of chitinous material through preformed pathways. These pathways may be in part located where during earlier phylogenetic (or also ontogenetic) development such cross veins were present. But mechanical forces associated with the shortening of the wings, for example, or the attachment of two longitudinal veins during development may also explain another part of these variations.

PHYLOGENY

GENERAL OUTLINE OF THE PHYLOGENY OF COREOIDEA (HETEROPTERA)

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The main criteria of classification are consistency with phylogeny, maximum informativeness and proportions of gaps between coordinate taxa. With these in mind, the following classification of trichophorous bugs at superfamily and family level is proposed:

1. Idiostoloidea: Idiostolidae;
2. Piesmatoidea: Piesmatidae;
3. Coreoidea (incl. Lygaeoidea and Pyrrhocoroidea): Colobathristidae, Berytidae, Malcidae (incl. Chauliopinae), Lygaeidae (incl. Cyminae), Largidae (incl. Physopeltinae), Pyrrhocoridae, Hyocephalidae, Stenocephalidae, Coreidae (incl. Alydinae), Rhopalidae;
4. Pentatomoidea: Thaumastellidae, etc.

Idiostoloidea are probably descendants of a group ancestral to the whole trichophorous stock. Pentatomoidea differentiated at the time when their ancestral species still had lygaeid-like facies, which has been retained only in Thaumastellidae of all the modern representatives. Piesmatoidea are related to Coreoidea, but evolved probably before the differentiation of modern coreoid families. There are no features enabling division of Coreoidea into 2 or more superfamilies with appropriate gaps.

All evolutionary lines of Coreoidea evolved from extinct Lygaeidae. While other families of Coreoidea are of a clade nature, Lygaeidae have explicitly grade character. Some modern lygaeid subfamilies share relatively more recent common ancestry with non-lygaeid families than with the other subfamilies of Lygaeidae. Thus Lygaeidae form a stem-group of Coreoidea. This fact does not mean a necessity of splitting this taxon, since coordinate grade and clade groups must always coexist in any universal classification.

The mosaic type of evolutionary trend is characteristic for Lygaeidae as well as for the other evolutionary lines of Coreoidea. The trends are mostly not interdependent and were not realised in full complement in all members of the same evolutionary line. The common appearance of the trends in a certain group of taxa, compared with their singular and convergent occurrence elsewhere, proves the common ancestry of the respective taxa.

The malcid evolutionary line evolved from the precymine lygaeids. The lygaeid subfamily Cyminae, particularly its tribe Ninini, shares many common trends with Malcidae and closely related Berytidae. The family Colobathristidae has the same ancestry, but differentiated probably earlier than the other groups of the line. The preischnorhynchine lygaeids were ancestral to precymines, and the type of stridulation occurring in the modern ischnorhynchine genus *Kleidocerys* Westw. was probably shared by the common ancestors of Pentatomoidea, Coreoidea, and Piesmatoidea.

The largid evolutionary line evolved together with the lygaeid subfamily Megalonotinae from premegalonotines. Largidae are a rather primitive family and from the subfamily Larginae evolved probably Physopeltinae and from prelargines the Pyrrhocoridae.

It is probable that also the coreid evolutionary line evolved from extinct Lygaeidae. Some indications suggest the premegalonotine ancestry of this line, and the fact that the same trends appear in the advanced members of both largid and coreid lines supports this hypothesis. Hyocephalidae and Stenocephalidae are the most primitive families of this line, and the advanced Coreidae must have passed through this structural level. Rhopalidae belong to the same line, but may have had a different evolutionary history from Coreidae.

ECOLOGY AND NATURE OF TAXONOMICAL FEATURES

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In studies of function and ecological meaning of basic taxonomic features the biological estimation of phylogenetic changes was found considerably to facilitate our understanding of phylogeny.

The Sarcophagidae present new material for investigation. It was consideration of the ecological features that helped us to understand the phylogenetical relations of subfamilies and genera. The consideration of only morphological features without any ecological explanation has shown a scale of differences, but has shed no light on evolution and phylogenetical causes.

Two subfamilies—Sarcophaginae and Miltogrammatinae, are the most widespread and comprise many species. Their features, ecology and habits are quite different.

The characters of Sarcophaginae (dark body colour, not very rapid flight, well developed running) are in conformity with their conditions of life, that is living under humid conditions with low insolation. Under conditions of strong insolation, all these features are harmful and always change in due course. For example, the desert Agriini (some species of the genus *Wohlfahrtia* and allies) have developed a thick white dust on the body, and increased the speed of flight. But the ever present feature in the Sarcophaginae is development of strong legs and big antennae with long arista in combination with small eyes. There is undoubtedly a connection between the size of the antennae and the chemoreceptors that reflects the way of life of the larvae in various decaying substrata. To find this medium it is necessary for the winged stages to have a well developed sense of smell as well as strong legs for running.

The morphological features of the Miltogrammatinae conform well with their life in open, well insolated conditions. These are: pale body colour, very rapid flight, weak legs, very big eyes and relatively short antennae (especially the arista). These features of sight and rapid flight are connected with the habits of reproduction—searching for and pursuit of hymenopterous hosts and larviposition in their nests.

The biological connection with static rotten substrata is very typical of the Sarcophaginae under moderately insolated conditions which cause the development of the sense of smell and running. These factors determine very rapid larval development (because of the ephemeral existence of such food substrata), monotonous external appearance (little importance of sight under such conditions), strong legs (necessity of moving on food surfaces for nutrition and larviposition) and moderately developed eyes, strongly developed pulvilli, arista and palpi (good development of sensoria, especially chemoreceptors). On the whole, the evolution of the Sarcophaginae reflects the improvement of larval development and the function of smell.

The Miltogrammatinae and Hymenoptera Aculeata are ecologically closely related as they live in conditions of strong insolation, that call for well developed sight and perfect flight. These conditions account for variation in appearance—pale body colour, often of mirror-type, small body size (ecological connection with the nests of host insects), and the development of rapid flight and the corresponding type of wings (developed as a result of living under hot soil conditions). The evolution of the Miltogrammatinae, on the whole, reflects improvement of the adaptations of the larvae for a life in subterranean nests of Hymenoptera. The main features are improvement of flight and sight, larvae and chemoreceptors showing little change.

The present investigation shows the importance of consideration of taxonomic relations of any group of animals in terms of ecological and functional relations, thus accounting for the causes and directions of phylogenetical development, and elucidating the very essence of evolution.

DIE BEZIEHUNGEN ZWISCHEN DER PHYLOGENETISCH-SYSTEMATISCHEN GLIEDERUNG UND DER LARVEN-LEBENSWEISE BEI DEN LONCHAEIDAE

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Nachdem die systematische Stellung der Lonchaeidae innerhalb der Pallopteroidea gesichert erscheint, gewinnt die Frage an Interesse, ob die eine oder andere Pallopteridae-Gattung mit den Lonchaeidae näher verwandt ist. Untersuchungen über die als Larven unter Baumrinde lebenden Pallopteridae deuten zunächst nur auf engere Beziehungen jener Pallopteridae zu den Lonchaeidae hin, deren Larven diesen Lebensraum bewohnen und deren Imagines wenig oder gar nicht gefleckte Flügel aufweisen.

Während in letzter Zeit der männliche Kopulationsapparat und der weibliche Ovipositor eingehend zur Deutung der Entwicklungsrichtungen innerhalb der Familie untersucht wurden, schienen zunächst die verschiedenen Lebensweisen keine deutliche Korrelation mit den so aus morphologischen Beziehungen abgeleiteten Verwandtschaftsverhältnissen zu zeigen. Daraufhin wurde jetzt ausgehend von der Lebensweise der Larven eine Prüfung der auf diese Weise getroffenen systematischen Gliederung vorgenommen, zumal gerade die Lonchaeidae mit ihrer Stenomorphie der Imagines gegenüber der verschiedenartigen Lebensweise ihrer Larven zu einer solchen Revision reizen.

Für die palaearktischen Arten lassen sich die Lebensweisen in drei Gruppen zusammenfassen, wovon die saprophage Lebensweise unter Baumrinde als ursprünglich angesehen wird. Eine Gallbildung an Gräsern, der Übergang der Larven zu einem Leben in Früchten und anderen Pflanzenteilen, wie Koniferenzapfen, sowie eine räuberische Ernährung unter Baumrinde werden als apoöke Lebensgewohnheiten gedeutet.

Die auf Grund der neueren morphologischen Untersuchungen ausgeschiedenen drei Unterfamilien lassen sich von den Lebensweisen her nicht begründen. Auffällig ist indessen bei den Dasiopinae die Übereinstimmung in dem Vorhandensein apomorpher Kennzeichen und der am weitesten spezialisierten Lebensweise der Gallbildung bei gleichzeitiger Erhaltung aller primitiven morphologischen Merkmale und der ursprünglichen, saprophagen Lebensweise unter Baumrinde.

Sechs der neun Lonchaeidae-Gattungen der Palaearktis finden zumindest teilweise auch in Verschiedenheiten respektive Spezialisierungen der Lebensweise eine Bestätigung: *Chaetolonchaea*, *Earomyia*, *Lamprolonchaea*, *Silba*, *Setisquamalonchaea* und *Lonchaea*.

Die Prüfung der Beziehungen zwischen der Lebensweise und der durch morphologische Ähnlichkeitsverhältnisse getroffenen Gliederung innerhalb der Gattungen ist besonders aufschlußreich im Genus *Dasiops* und in der artenreichsten Gattung *Lonchaea*. Zwei Hauptzweige charakterisieren die Entwicklung in der Gattung *Dasiops:* Von dem einen Weg spalteten sich Artengruppen mit einer plesioöken, saprophagen Lebensweise teilweise unter Laubholzrinde ab, während der andere Zweig die Tendenz zu extrem spezialisierter Lebensweise (Gallbildung) aufweist.

In der Gattung *Lonchaea* führt eine Untersuchung der verschiedenen Formen der Lebensweisen in dem in der Palaearktis fast einheitlichen Lebensraum der Larven (Baumrinde) zu dem gleichen Ergebnis wie eine Prüfung der morphologischen Ähnlichkeitsverhältnisse: Es resultieren zwei Evolutionswege. Von der Lebensweise her betrachtet, entwickelte der eine mit dem Nadelwald verbundene Artengruppen gegenüber einer vorwiegend mit dem Laubwald verknüpften Lebensweise der Arten des anderen Zweiges.

Begonnene Untersuchungen über die Zusammensetzung der Begleitfauna jener Artengruppen der Lonchaeidae und Pallopteridae, deren Larven unter Baumrinde leben, ergaben die Beobachtung, daß einige Artengruppen mit großer Konstanz auch durch "Charakterarten" ihrer Begleitfauna eine eigentümliche Bestätigung finden, was möglicherweise die Berechtigung der getroffenen Gliederung zusätzlich fundiert. Als solche "Charakterarten" erwiesen sich für die Lonchaeidae und Pallopteridae vor allem einige Drosophilidae aus den Gattungen *Stegana* und *Chymomyza* sowie für die Lonchaeidae eine Pallopteride, deren Auftreten bestimmte Artengruppen mit großer Beständigkeit begleitet. Inwieweit solche Beziehungen Verwandtschaftsverhältnisse widerzuspiegeln vermögen, bedarf weiterer Untersuchungen, doch dürften sie möglicherweise zumindest einen zusätzlichen Weg zum Erkennen derselben bieten.

ON THE EPIZOIC ASSOCIATIONS OF CHIRONOMIDAE (DIPTERA) AND THEIR PHYLETIC RELATIONSHIPS

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In the Dipterous family Chironomidae the larval stages are adapted to various ways of life and to several kinds of nutrition. Among members of the subfamiliae Orthocladiinae and Chironominae, there are some larval types which live in association with other water animals and have developed special feeding habits. All genera involved, their types of association, and the host groups are listed in Table I.

SUBFAMILIAE	TRIBUS	GENERA	HOST GROUP	KIND OF ASSOCIATION
ORTHOCLADIINAE	Orthocladiini	Cardiocladius	Diptera: Simuliidae	paroecious
		Symbiocladius	Ephemeroptera: Ecdyonuridae	ectoparasitic
		Genus incertum (≠ Orthocladius)	Diptera: Blepharoceridae	phoretic
		Plecopteracoluthus	Plecoptera: Perlidae	phoretic
		Genus incertum	Trichoptera: Limnophilidae	inquilinic
	Metriocnemini	Epoicocladius	Ephemeroptera: Ephemeridae	phoretic
CHIRONOMINAE	Chironomini	Xenochironomus	Spongia	endoparasitic
		Demeijerea	Spongia	endoparasitic
		Genus incertum	Spongia	epioecious
		Chironomus (s.l.?)	Bryozoa	inquilinic
		Parachironomus	Bryozoa	commensalic
		Parachironomus	Mollusca	endoparasitic ectoparasitic

Table 1.
Associations within Orthocladiinae and Chironominae.

Only a few species are known within every genus, generally all of the same life pattern. They replace one another geographically, and are associated with different but related host species.

Morphological and ethological studies have shown that there is no close relationship between any of the above genera. Within the Orthocladiini and the Metriocnemini, each genus including epizoic species seems to be closely related to genera of non-epizoic species. Thus, it may be stated that each genus of epizoic Orthocladiinae has taken its origin independently from different non-epizoic ancestors. Almost all have progressed on a different evolutionary path in association with a different host group. Each apotypical pattern seems to have developed independently from the other, and directly out of a plesiotypical one. Thus Henson's assumption (1956), that phoretic associations "grade into truly parasitic associations and reveal how these latter could have arisen by an evolutionary process" is incorrect for the Orthocladiinae. At least in this subfamily, phoresis does not represent a certain grade on the evolutionary path to parasitism, and parasitism has not necessarily developed by the way of phoresis. Rather, we can state that the members of Orthocladiinae whose larvae live parasitically on other water insects have developed from forms whose larvae lived predaciously without, primarily, being associated closely with their prey. Others however, the life patterns

of which we call phoresis, inquilinism, or commensalism, most probably have taken their origin from algae- or detritus-feeders. Even with genera of one and the same life pattern, there is no evidence for a close relationship. This means that a certain manner of living and feeding has arisen several times from different sources. Each species of the genera *Symbiocladius* and *Epoicocladius* is limited to a different subregion of the northern hemisphere. This pattern of distribution indicates a rather early origin of epizoic life in these genera and its establishment long before the separation of the continents inhabited by them. The situation in Chironominae may be similar to that in Orthocladiinae. A precise decision, however, cannot yet be made because of the ignorance of the systematic position of the genera in question. Thus, it would be conceivable, that in this subfamily parasitism, for instance on *Spongia*, has developed by the way of commensalism and inquilinism. Generally however, we may say that in Chironomidae phoresis and parasitism are distinct apotypical life patterns which have arisen independently, in parallel, and repeatedly from different sources of plesiotypical feeding habits.

PHYLOGENETIC CONSIDERATION OF THE *VALGUS* GROUP OF BEETLES, BASED ON THE LARVAL CHARACTERS

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The *Valgus*-group of beetles has usually been treated as subfamily Valginae of the family Cetoniidae, or as a tribe Valgini of the subfamily Cetoniinae in the Pleurostict Scarabaeidae. Of this group a few hundred species are known to entomologists. *Valgus hemipterus* is a representative of the group in which all developmental stages are found in the buried and decaying parts of stakes of *Acacia* and other woods. Ritcher has described the North American species *Valgus canaliculatus* and *V. seticollis;* the larvae and adults of these species occurred in termite galleries in a soft-maple log and a beech log respectively. I have found all larval stages and adult females of the Japanese *Nipponovalgus angusticollis* in decaying pine trees and other woods.

The *Valgus*-group seems to me to be an isolated and simplified one in the Pleurostict Lamellicornia, when due consideration is given to the larval characters listed below, and to be referrable to a new family Valgidae:—(1). In the family Valgidae the body is rather slender and these larvae usually walk on the substrate, using their legs for this purpose. In the Cetoniidae *sensu restricto* the body is very stout and the larvae move upside down by means of body contractions. (2). The spiracles are small and faint, especially those of the abdomen. (3). The small dorsum of the tenth abdominal segment is divided by a slight median longitudinal groove into two oval cushion-like areas. (4). The anal-slit is traversed by a groove and the border of the dorsal anal lobe is distinct. (5). The raster is absent and the setation is limited to a few slender fine setae. (6). The brownish enlargement of the epicranial suture (the site of the lamella for muscle attachment) extends beyond the frontal suture into the frons. (7). The epipharynx, especially as regards the tormae, is almost symmetrical; the haptomerum is entirely absent and the haptolachus is slightly developed, without any nesium. (8). The stridulating area on the mandible is indistinct or absent. The cutting edge of each mandible is bidentate, the distal tooth formed by the fusion of two primary teeth. In the Cetoniidae and the Trichiidae the two primary distal teeth are not fused and a fourth tooth is present on the left mandible. The molar part of the mandible has neither brustia nor acia and the heel is fused with the proximal lobe to form an acute posterior process. (9). The maxillary stridulating teeth are absent although a few faint wrinkles and a minute anterior tubercle may be discerned. The galeal uncus is present but the lacinial uncus is absent. The maxillary palp consists of three segments. (10). The hypopharyngeal sclerome is almost symmetrical and is evenly sclerotized, including both lateral lobes. There are neither setae nor phoba-like processes. (11). The apical segment of the antenna bears a large, elliptical sensory spot on the dorsal and on the ventral surface. (12). The three pairs of legs are almost identical in form; the tarsungulus is sharply pointed and very slightly falcate.

SOME FUNCTIONAL ASPECTS OF PHYLOGENY IN THE ADEPHAGA (COLEOPTERA)

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Many features of the coxae and headcapsules of species of Adephaga can be correlated with differing modes of life and are of much interest when considering the phylogeny of the Adephaga.

Front coxae: Besides the main pleural and trochantinal articulations of Carabidae, a sternal articulation is formed by a coxal peg held in a socket in the prosternal inter-coxal process (fig. 1A). A well developed peg is also present in *Haliplus*, *Hygrobia* and *Amphizoa*, but it is minute in Hydroporinae and absent in those Dytiscini and Laccophilini studied. Crowson suggested that the peculiar structure of the Adephagid hind coxa was originally an adaptation to a predacious life under bark, etc., where the hind leg would only move in one plane. This would also explain the sternal articulation of the Carabid front coxa. In higher Dytiscids, loss of the coxal peg may be correlated with the change in function of the front legs from the propulsive organs of the ancestral Adephaga to mobile organs for grasping the prey. The front coxae are exserted in both Paussids, where the sternal articulation is lost,

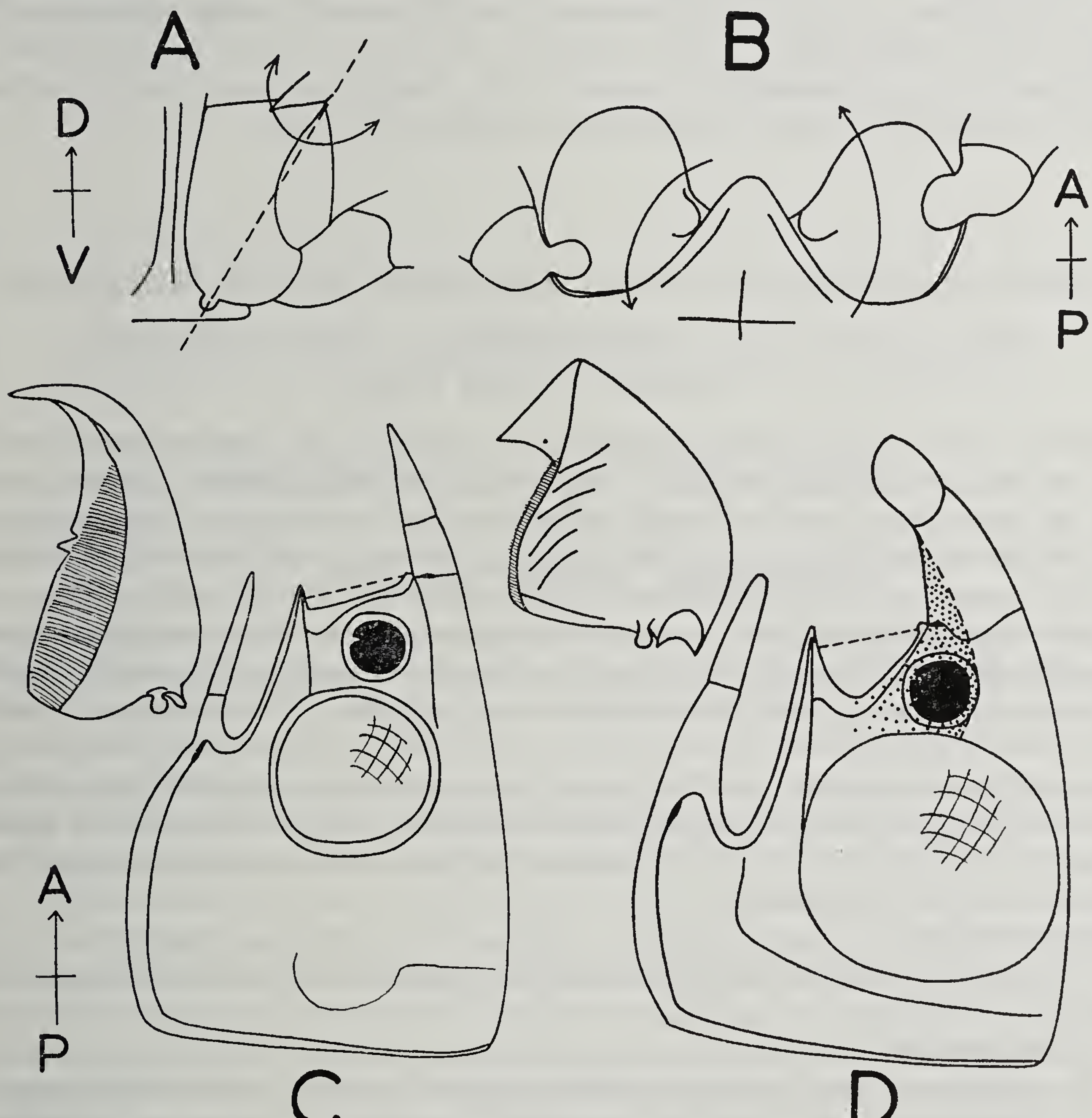

Fig. 1. (*a*) diagrammatic posterior view of right front coxa of *Carabus* to show sternal articulation; (*b*) ventral view of second coxa of *Carabus* to show ventral flanges; (*c*) diagrammatic side view of Carabid head (mandibles and maxillae missing) to show mandibular articulations; (*d*) as (*c*) for Dytiscid head and mandible. Anterior (A), posterior (P), dorsal (D) and ventral (V) directions shown.

and Cicindelids, where it is strong but has moved dorso-mesally. The presence of the articulation in the Adephagid stock is suggested by its presence in *Rhysodes*.

Middle coxae: The ventral "buffer-stop" described by Jeannel in Carabids may also act as a sternal articulation. It is usually a semi-circular flange which forms a poor articulation with the meso-metasternal union (fig. 1B). In some Carabidae (e.g. *Drypta*), the flange almost forms a condyle. A true condyle with a good sternal socket is found in Cicindelinae, *Omophron* and *Haliplus*, although detailed differences suggest parallel evolution. In contrast to *Haliplus*, the coxal flange is absent in most water beetles, and this is also true of *Trachypachus*, *Metrius*, Paussinae and *Rhysodes*. This suggests that Carabids may have developed the mesocoxal flange after the Dytiscid stock had diverged.

Head: In contrast to the Carabidae (fig. 1C), the head in the Dytiscidae (fig. 1D) is part of a body streamlined for efficient swimming. The "eye-brow" ridge is strongly developed and covers the antennal base. The lateral extension of the mandibles during prey capture has been reduced without altering the gape by moving the mandibular articulations mesally. This modification of the mandible is accommodated by the emargination of the head capsule between the anterior and posterior mandibular articulations. *Hygrobia* and *Amphizoa* are basically similar, but *Haliplus* has a much more Carabid-like head.

An important but little studied character is the mid-gular apodeme, which is a median vertical flange developed on the head floor of many Adephaga to provide origin for the labial muscles. Its widespread occurrence suggests that it is an ancestral feature which has been lost in several groups. It is absent in Dytiscidae and *Hygrobia*, but present in *Amphizoa*, *Noterus* and Gyrinidae. It is absent in most of the "Carabine" tribes, in Scaritini, Broscini, and in most of the "Lebiomorph" tribes, although *Masoreus* and some Lebiini retain it. The loss of this apodeme is presumably correlated with changes in head structure affecting the angle of pull of the labial muscles, and the space available for them.

COXAL CAVITIES AND THE PHYLOGENY OF THE ADEPHAGA

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The coxal cavities of the Coleoptera have been formed by the outward growth of shelf-like extensions on the surrounding sclerites, to form a rim or wall, partially concealing the coxa. Probably all three pairs were originally alike, bounded anteriorly by the sternum of the segment to which the leg belongs, and posteriorly by the sternum of the next posterior segment. A part of the lateral boundary was formed by the epimeron. At the midline, the two cavities of each pair were confluent, but in ventral view they appeared separated, since a median sternal process extended ventrally and posterior between them, until it met or overlapped a median presternal process from the next posterior segment. The mesocoxal cavities have been most conservative, while the metacoxal cavities have been modified by the transverse enlargement of the metacoxae, and the procoxal cavities have been modified by the evolution of a more flexible joint between the prothorax and mesothorax. Many further modifications have occurred in the structure of all three pairs of cavities. The distribution of the major types is presented in outline form below:

I. Mesocoxal cavity:
   A. Lateral Rim: (As the distribution of these types is well known, it will not be repeated here.)
   B. Mesal margin:
      1. Confluent type (cavities separated only superficially): Most Adephaga.
      2. Separated type (cavities completely separated): Ozaenini, Metriini, Omophronini.

II. Metacoxal cavity:
   A. Lateral margin:
      1. Disjunct type (metepimeron reaching outer edge of coxal cavity but not overlapping abdomen): Scaritini, Cicindelini, Loricerini, Elaphrini.

2. Conjunct type (metepimeron eliminated): Carabini, Cychrini, Nebriini and relatives, Omophronini, Promecognathini.
3. Lobate or Disjunct-Lobate type (metepimeron forming shelf, overlapping abdomen): Ozaenini, Metriini and the "Harpalinae" of Leconte.
4. Incomplete type (metacoxa reaching lateral margin of body): Trachypachidini, Hydradephaga, Gehringiini, Rhysodini.

B. Mesal margin:
1. Confluent type: Most Adephaga
2. Separated type: Gehringiini, Rhysodini.

III. Procoxal cavity: Lateral margin always disjunct. Mesal and hind margins furnish three pairs of criteria for classification: confluent vs. separated; open vs. closed; and bridged vs. unbridged. Closed cavities have a *postcoxal bar*, formed by interlocking processes from the proepimeron and prosternum. Bridged cavities have a *postcoxal bridge*, a sclerotization of the primary body wall posterior to the coxa. These criteria are known to occur in five combinations.

Extensive parallelism makes it impossible to use single features of the coxal cavities as the basis for a natural classification. When considered in conjunction with other characters, coxal cavities provide clues to phylogeny. In particular, the procoxal and metacoxal cavities, as well as the glabrous antennae, suggest that Trachypachydini are really related to the Hydradephaga. Since the structure of the antenna-cleaner and the chaetotaxy of the labrum link Trachypachidini to Ozaenini and Metriini, it seems probable that the aquatic families of Adephaga are really highly modified Isochaetous Carabidae.

NOMENCLATURE. SUBSPECIATION AND SPECIATION

ENTOMOLOGICAL NOMENCLATURE

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Nomenclature is a much derided subject, but some system of nomenclature is inevitable for purposes of recording, filing, recovering, exchanging, and discussing information. With nomenclature come rules, i.e., some kind of a systematic approach, to avoid chaos, promote stability, and provide for orderly change.

Botanical and zoological codes have long been separate, and in recent years a code for microbiology has been developed. Codes for entomology have been proposed, at least as far back as 1778, but none has ever had official sanction.

Most of the rules of the new International Code of Zoological Nomenclature (1961) are common to entomology and the rest of zoology. There are the standard general rules pertaining to punctuation and the acceptance of 1758 as a nomenclatural starting point. There are long-standing rules from the old Code such as those for the designation of type-species, and there are a few disputed rules (e.g., secondary homonymy, neotypes), objections to which cut across the whole field of zoology. Because of the broad common ground, then, a separate Entomological Code seems unnecessary.

The Zoological Code treats 3 subjects which are specially important to entomology: Infrasubspecific names, names founded on the work of an animal, and Article 23b, the Limitation on the Law of Priority. The first two are significant chiefly because of the proportionally large number of insect names. However, in both subjects the Code will suffice for entomologists and can be accepted by them.

Article 23b is a different matter. The Nomenclature Committee and Section A of the Entomological Society of America petition the International Congress of Entomology to propose and strongly recommend to the International Commission on Zoological Nomenclature that the Code be amended to exempt the field of entomology from the provisions of paragraph b of Article 23. Priority is considered to be the most effective and efficient approach to the mass of literature and millions of names with which entomologists must deal. Difficulties and confusion can be dealt with by use of the plenary powers.

SOME THOUGHTS ON SPECIATION IN INSECTS

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The number of species in the class Insecta is much larger than the total number of species of all other kinds of animals put together. It appears that the peculiar combination of two main characters, the chitinous exoskeleton and aerial mode of life, has probably been the largest contributor to so much speciation in insects. It appears that due to the mechanical rigidity of chitinous exoskeleton, comparatively minute variations in the external genitalia lead to reproductive isolation and consequent fixation of the species. This factor alone, however, cannot explain the large amount of speciation in insects because other classes of Arthropoda having similar exoskeletons do not have as many species. Hence, it is further surmised that the development of the aerial mode of existence, specially the acquisition of wings leading to life under much more diverse ecological habitats, has provided the trigger for variations.

These considerations invite speculation on the wider aspects of species and speciation in general. It is generally agreed that the most definitive criterion for distinguishing two distinct species is that they do not interbreed. But even this appears to fail in a number of cases wherein it has been possible to obtain fertile hybrids not only between different species but even between different genera. The recorded cases are more from the plant kingdom than from the animal kingdom. These successful cases of hybridisation between different species and different genera inevitably lead to the conclusion that the reproductive isolation in different species is not always due to the fact that the male gamete of one cannot fertilise the female gamete of the other. Various possible mechanisms of reproductive isolation leading to speciation may be:

(*a*) GEOGRAPHICAL ISOLATION.

(*b*) SIMPLE PHYSIOLOGICAL ISOLATION:—When the two species do not interbreed in nature because they come to maturity at different times.

(*c*) MORPHOLOGICAL ISOLATION:—Comparatively minor variation in the genital armature eliminating chance of successful copulation.

(*d*) PROTOPLASMIC INCOMPATIBILITY can be said to exist when all other simple and apparent causes of reproductive isolation are removed and even then interbreeding cannot be achieved.

There may be several other factors responsible for reproductive isolation. However, the important implications of these ideas are that different species need not be reproductively isolated due to what has been called protoplasmic incompatibility and that it should be easily possible to overcome other causes of reproductive isolation. If this line of thought is sound then it should open immense possibilities for hybridisation specially by the techniques of artificial insemination and cross fertilisation. In addition the boundaries between different species become still more shaky and the life current flowing through different species becomes more continuous.

SUBSPECIATION ET POLYMORPHISME CHEZ *NEPHERONIA ARGIA* FABR. (LEP. PIERIDAE)

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Les coupes subspécifiques de cette espèce sont traditionnellement basées sur les ♂ par suite de la complexité du polymorphisme des ♀. D'après les ♂ on peut distinguer avec Stoneham, 1957:

(1) *N.a.argia* de l' ouest africain au Kivu
(2) *N.a.argiolisa* de l'Ouganda au Nyassaland
(3) *N.a.varia* de l'Afrique du Sud

Il était intéressant de comparer cette variation des ♂ avec celle des ♀, ce que j'ai effectué avec les matériaux du Muséum de Paris, du British Museum (N.H.) et du Muséum de Tervuren. On constate que le polymorphisme des ♀ (dont on trouvera les caractères distinctifs des différentes morphes dans les travaux d'Aurivillius, 1895, de Suffert, 1904 et de Van Son, 1949) présente une nette variation géographique:

(1) les mph. *argia, poppea, idotea, sulphurea* se trouvent de l'ouest africain jusqu' à l'ouest du Kénya;

(2) les mph. *semiflava, mixta* ainsi qu'une morphe "orangée", inédite se trouvent au centre de l'aire précédente mais manquent à la périphérie, cas classique en polymorphisme géographique.

(3) la mph. *mhondana* se trouve seulement dans l'est africain et les mph. *varia, oraria* et *hemicrocea* seulement dans le sud africain.

(4) les mph. *aurora* et *giara* se trouvent à la fois dans l'est et le sud africain.

En tenant compte en outre de l'extension des dessins foncés des ♀ on doit ainsi reconnaître quatre sous-espèces au lieu de trois:

(1) *N.a.argia* de l'ouest africain au Kivu—♂ ♀ dessins noirs étendus; ♀ à polymorphisme "occidental" (mph. *argia, poppea, idotea, sulphurea, semiflava* et "orangée", les trois dernières absentes de l'ouest de l'aire).

(2) *N.a.argiolisa* de l'Ouganda et de l'ouest du Kénya—♂ dessins noirs relativement réduits; ♀ dessins étendus, à peine moins développés que ceux de *N.a.argia*, a polymorphisme "occidental" expurgé (mph. *argia, poppea, idotea, sulphurea*).

(3) *N.a.mhondana* du Kénya (sauf ouest) au Nyassaland—♂ dessins noirs relativement réduits, *indistinguables de ceux de la sous-espèce précédente:* ♀ dessins relativement réduits, à polymorphisme "oriental" (mph. *mhondana* caractéristique, mph *aurora* et *giara* en commun avec *N.a.varia*).

(4) *N.a.varia* du Sud africain—♂♀ à dessins noirs réduits, ♀ à polymorphisme "méridional" (mph. *varia, aurora, hemicrocea* caractéristiques; mph. *aurora* et *giara* en commun avec *N.a. mhondana*).

Soulignons un phénomène particulièrement remarquable: les populations de l'Uganda et de l'ouest du Kénya consistent en ♂ à *habitus "oriental" et en ♀ à habitus et à polymorphisme "occidental"*.

L'intreprétation de ce phénomène est délicate. Dans les limites de la place disponible indiquons seulement que l'hypothèse la plus vraisemblable est que les populations isolées ici sous le nom de *N.a.argiolisa* sont étroitement apparentées a celles de l'ouest africain (*N.a.argia*) et nullement à celles de l'est africain (*N.a.mhondana*) comme cela était admis jusqu'ici. Cela est démontré a mon avis par l'habitus des ♀, le sexe "le plus conservateur", à dessins noirs à peine plus réduits que ceux de *N.a.argia* et à polymorphisme "occidental" tandis que les ♂ doivent avoir acquis indépendamment un habitus indistinguable de celui de *N.a.mhondana*, conformément à la règle éco-géographique de Glöger.

PARTHENOGENESIS AND SPECIATION IN *OPHRYASTES*, A GENUS ENDEMIC TO THE NEW WORLD (COLEOPTERA: CURCULIONIDAE)

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The genus *Ophryastes* Schoenherr contains 43 species of large, flightless, broad nose weevils occurring in arid regions of western North America. The species show much individual variation in coloration and structure and are hard to define. A set of structural characters involving male and female genitalia, head and rostrum, proventriculus, apex of hind tibia, and prothorax was proposed to define a species. On the basis of proventricular armature the genus is unique from a world standpoint.

The *Ophryastes sordidus* complex contains five species, three are presumably parthenogenetic, one (*sordidus* LeConte) is both parthenogenetic and bisexual, and one is only bisexual. The species in this complex are easily separated by their distinctive female genitalia. In distribution *sordidus* occupies a central range of some 120,000 square miles while the other species are arranged peripherally with ranges at least one order of magnitude smaller. Among populations of parthenogenetic *sordidus* from Arizona and Utah it was noted that some exhibit polymorphism of the spermatheca; in two cases both normal and mutant types of spermathecae occur in the same population, in one case only the mutant type was detected.

The *Ophryastes decipiens* complex contains six species, one of which is believed to be parthenogenetic. In contrast to the *sordidus* group the species appear to be arranged along an East-West axis. The species of this complex are difficult to separate. No differences in the structure of the female genitalia were found and other, less satisfactory characters such as separation of head from rostrum were utilized.

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BIOCHEMICAL AIDS TO TAXONOMY

SEROLOGICAL SYSTEMATICS OF INSECTS

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Serological analyses are being made of the ontogeny, systematics, and genetics of insects. The methods used compel comparisons among protein molecules that are capable of inducing the formation of antibodies and of reacting *in vitro* with them in measurable ways. The immunochemical data acquired permit conclusions on the qualitative and quantitative correspondences among the molecular homologues of organisms. Serological studies provide insight into the molecular environments of developing insects and new perspectives on their systematics and genetics.

ANTIGENS AND ANTISERA. Most serological studies on insects have employed saline extracts of whole bodies as the antigens to be injected into rabbits. Insect hemolymph, saline and alcoholic extracts of cuticle and other special body parts, and extracts of delipified insect materials are examples of more specialized preparations that also have been employed. Nine to 12 proteins are regularly found in insect hemolymph or in saline extracts of whole bodies. Extracts tend to blacken because of the usual presence of tyrosinase which acts to cause the formation of melanin. Chemical inhibitors such as KCN, phenythiourea, and ascorbic acid are useful but not completely satisfactory because the concentrations required to completely control the enzyme adversely affect the serological reactions.

Antisera, almost always produced in rabbits, are used as analytic reagents to measure the biochemical similarities and differences among insect proteins. Rabbits produce antisera of differing specificities and, accordingly, may be taxonomic "lumpers" or "splitters" depending upon the capacities of their antibodies to discriminate among proteins related to the injected antigen. The serological principle of "quantitative specificity" (4) implies that the injected antigen is the most reactive with an antiserum and that other proteins cross-react in accordance with their chemical similarity to the reference or homologous antigen.

The precipitin reaction has proved to be the most useful serological test in the comparison of insect proteins. In *liquid systems* the reactivity of a serial dilution sequence of antigen is measured in terms of antigen titer (2) or turbidimetrically in terms of total amounts of precipitate formed (5). In *gel systems* (11, 14, 15) the antigen-antibody precipitates form discrete zones and make it possible to relate serological reactions to particular proteins—a distinct advantage in systematic studies.

ONTOGENY. Immunoembryological work has been done on five holometabolous insects: the cecropia and cynthia silkmoths (12, 16), the honeybee (1), the housefly (8), and the yellow mealworm (6). On the basis of the serological work the following generalizations are possible:

1. Species-characteristic antigens occur and are those that exist in every stage of the life cycle.
2. The adult always has a stage-characteristic protein present.
3. One of the antigens present is sex-limited to females.
4. A transitory molting protein appears immediately before each molt of the larva.
5. Antigens vary in number of kinds at each stage of the life cycle.
6. The amount of each kind of protein varies from stage to stage of the life cycle.
7. Qualitative changes occur in some of the proteins during ontogeny.

SYSTEMATICS. Serological systematics of insects began in 1915. In the 50 year period since then not more than 150 species have been studied, by 15 workers. Except for one paper in which 13 species of wingless insects were compared, serological comparisons have been only among winged insects. Generally, families have been represented by one to three species. The families most represented have been the Blattidae (7 species) and Acrididae

(10 species) of the Orthoptera, the Culicidae (9 species) and Drosophilidae (12 species) of the Diptera, and the Tenthredinidae (6 species) of the Hymenoptera.

Early serological workers used only comparisons of antigen titers. Families were distinguished readily, subfamilies with difficulty, but genera and smaller taxa within a subfamily not at all. Improved serological methods quickly permitted workers to distinguish species within a genus.

Significant contributions of serology to studies on the systematics of organisms include the following:

1. A "serological yardstick" (3) for measuring relationships between taxa results from turbidimetric precipitin tests. For example, within the genus *Melanoplus* species are 55% similar; genera within the family Acrididae are 28% related; interfamily relationships within the order Orthoptera have values of 12% (13). For other groups of insects the values for the various taxa could well be different, but the hierarchical arrangement is constant.

2. Parallel orders of relationship among species are obtained when a variety of corresponding proteins are compared. For example, three kinds of proteins fractionated from saline extracts of species of mosquitoes in the genus *Aedes*, when compared serologically, yielded parallel classifications (9). Such data imply a greater orderliness of evolution at the protein molecular level than at the level of gross morphology.

3. Objective classifications are obtained in the sense that serological reactions do not reflect any bias of the investigator. For example, overlapping serological studies on the Blattidae by three independent workers (Leone; Pauly; and Downe) yielded completely consistent information on interrelationships among the genera of roaches tested.

4. Consistent relative placements are more readily obtained by serological than by comparative morphological means. When extensive serological and morphological studies on four *Drosophila* species were compared (7), both technics always ranked the same species second. Third-ranked species were more definite and precise in the serological comparisons. Fourth-ranked species were so graded by 65% of the serological tests and by 46% of the morphological characters. Serological rankings never placed a morphologically fourth-ranked species higher than third rank, yet some of the morphological characters placed the fourth-ranked species as high as second.

GENETICS. By means of absorption tests, serological distinctions have been made between mutant stocks of *Drosophila* and other Diptera. Similarly, males and females have been distinguished as well as rearrangements of euchromatin and heterochromatin (10). Initially studied were stocks of wild, white eye, and vestigial, and later, isogenic stocks of wild type and two coisogenic stocks, vermilion and ruby. Antigens common to all stocks and also antigens peculiar to each stock except ruby were found.

SUMMARY. There is probably no limit to the capacity of serological methods to recognize genetically known stocks of insects or to define taxa among natural populations. Ontogenetic studies on proteins reveal qualitative and quantitative changes that compel the limitation of comparisons among organisms to corresponding stages of life cycles when judgments are to be made on the systematics and evolution of insects at the molecular level.

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TECHNICAL PROGRESS IN THE SEPARATION AND IDENTIFICATION OF INSECT SERUM PROTEINS

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The usefulness of insect blood proteins for taxonomic studies increased considerably after the introduction of new techniques for the separation and identification of these proteins. The experiments are highly reproducible. Nevertheless, a number of variables deriving from the biological material should be taken into account.

Within certain limits the protein content of insect blood is more or less comparable to man, but still higher than in many other invertebrates. Florkin (9) was the first to make a comprehensive study of the hemolymph protein content of different groups of insects: Coleoptera 2·7-4·1%, Hymenoptera 5%, Orthoptera 1%, Lepidoptera (*Bombyx mori:* spinning larvae 4·5%, pupae 5·9%, adults 2%). These figures are based on pooled blood. Fluctuations in the protein concentration of insect blood were already observed (11).

For several years an inadequate terminology divided the hemolymph proteins into "albumins" and "globulins": Bishop, Briggs and Ronzoni found "albumin" and "globulin" in about equal concentration. Ducceschi (8) described two "globulins" and three "albumins" in *Bombyx mori.* Florkin and Duchâteau (10) found two "albumins" and one "globulin" in *Hydrophilus piceus.* Refined experimental tools have revealed the complex composition of insect blood.

1. *Paper electrophoresis.* Drilhon (7) found two larval proteins in *Bombyx mori.* Their concentrations increase during the fifth instar. When spinning starts, the region of the slow moving proteins (at pH 8·6) becomes more complex. After the cocoon is made, the fast band disappears almost completely. Larval blood proteins differ from imaginal proteins. Sexual differences were also observed.

2. *Agar gel electrophoresis.* Using only 1-3 μl of blood, Denucé and Rabaey (5) examined the following species (micro-technique on microscope slides): *Galleria mellonella* (spinning and non-spinning larvae), *Macrothylacia rubi, Phragmatobia fuliginosa, Tenebrio molitor* and *Dytiscus marginalis.* The separations were better than on filter paper. All species gave a different pattern. The sequence of various proteins in the gel was not always the same as in paper electrophoresis. The terminology from human hematology is not valid for a classification of insect serum proteins. As the affinity of these proteins for Amidoblack is still unknown, densitometry of the bands after staining is of relative value.

3. *Starch gel electrophoresis.* This medium gives very sharp separations. We reinvestigated the quantitative changes of the hemolymph proteins with this method (2, 3). As many as eleven proteins appeared in *Galleria mellonella* after staining with Amidoblack. During the voracious period all the proteins increased. Especially one fraction showed a considerable increase in concentration and predominated at the end of the voracious period, with two other strongly stained bands. The amount of insoluble protein increased during spinning. Two strong bands are predominant at this stage. We also repeated the experiments of Drilhon with *Bombyx mori,* using starch gel electrophoresis (3): only one protein can be visualized with Amido black in fourth instar larvae. It increased in fifth instar larvae. Two minor fractions appeared at the cathodic end. Spinning silkworms first show a further increase of the main protein, but its concentration soon diminishes. The fast moving proteins, and also a few components moving between the origin and the main protein increase. Like in *Galleria,* insoluble protein accumulates at the origin during pupation. Striking changes in the pattern were also observed with *Vanessa urticae* during larval and pupal development. Each of the following species of the family Lasio campidae showed a specific pattern: *Lasiocampa trifolii, Cosmotriche potatoria, Macrothylacia rubi* and *Malacosoma neustria.* Differences also appear between individual sera of less related families, such as *Euproctis chrysorrhaea, Dasychira fascelina Arctia caja, Apis mellifica* and *Melolontha vulgaris.* Laufer (15) compared the mobilities of hemolymph proteins of *Samia cynthia* and *Hyalophora cecropia.* Different electrophoretic mobilities do not exclude immunological cross reactivity (see below).

4. *Enzymatic reactions on electrophoresis strips.* A clean separation is not the ultimate goal. Identification and characterization of individual proteins must follow. Multiple polypheno-

loxidases were described in *Galleria mellonella, Macrothylacia rubi* and *Phragmatobia fuliginosa* (4, 6). Using the zymogram technique (12, 16), Laufer (13, 14) described the following enzymes in *Cecropia* blood: tyrosinase, chymotrypsin, sulfatase, galactosidase, esterase, phosphatase and several dehydrogenases. Recently, we found that one fast running esterase of *Bombyx mori* is much stronger in pupal than in larval blood. Three to four esterases could be visualized with α-naphthyl butyrate, α-naphthyl acetate and naphthol AS acetate as substrates. Alkaline phosphatase was much weaker.

5. *Immunological methods.* Advantage is taken of the high specificity of the antigen-antibody reaction. Telfer and Williams (19) found that each of the six antigens in the blood of the *Cecropia* silkworm varied in time and magnitude (agar diffusion method of Oudin), thus showing close relationship to morphogenetic events of metamorphosis. A seventh antigen was found in thousand times higher concentration in females than in males. It appears after the cocoon is spun (17). Telfer (18) observed a selective accumulation of this "female" protein in the oocytes. Laufer (15) reported a remarkable cross reactivity between electrophoretically fast moving esterases of *Hyalophora cecropia* and *Samia cynthia* blood. The enzyme accumulates at the end of the fifth instar, is found throughout pupal life and disappears in adults. An examination of the possible antigenic relationship of this enzyme with the fast moving esterase we have found in *Bombyx mori* would be of particular interest. Immunoelectrophoresis (method of Grabar and Williams) of *Bombyx mori* blood proteins using an antiserum against fifth instar larval blood shows alterations in the antigen pattern during metamorphosis, which are correlated with changes in the protein pattern as seen in regular zone electrophoresis.

The above data and references demonstrate that through refinement of the techniques for separation and identification, the study of hemolymph proteins may be very useful in taxonomy. However, considerable attention should be paid to genetic and environmental factors (20), developmental stage, sexual differences and age of the protein sample.

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MUSCLE PROTEINS AS PHYLETIC INDICATORS AMONG THE BEES*

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The use of electrophoresis as a systematic adjunct is not particularly new, having been in use for the past ten years. There has been, however, a remarkable refinement in techniques during the past few years which has permitted a considerable improvement in resolution and separation of the soluble protein fractions of body tissues.

There are almost as many variations in technique as there are investigators using it, but for convenience, all may be placed in one of two basic "types". These are: the moving boundary type of Tiselius; and zone electrophoresis using various supporting media such as paper, agar, starch block, cellulose acetate, starch and polyacrylamide. The starch gel method of Smithies (4) and the polyacrylamide gel method of Ornstein and Davis (3) appear to be the most sensitive of these.

The classical theory of free solution electrophoresis considers the electrophoretic mobility of a protein molecule to be the result of two physical forces: (*a*) the accelerating force which is the product of the electrical field strength and the charge of the molecule, and (*b*) a retarding force resulting from the viscosity of the medium and size of the migrating molecule. From this, it is apparent that two proteins which migrate together through a free solution field do not necessarily have the same molecular size, nor are the separate bands obtained necessarily composed of a single protein.

Gels have introduced the effect of pore size of the gel matrix as a physical factor. Although the gel matrix has increased the viscosity, it has had the effect of resolving protein solutions into individual components which are distributed throughout the gel in non-serial order with respect to their free solution pattern. The specific effects of the gel matrix are significantly dependent upon the concentration of the gel which may be modified to act in fashion analagous to a series of filters. Gels offer high resolution because of the effect of "pore-size" at the molecular level.

Besides the analysis of total extractable tissue proteins, there exists another potentially fruitful comparative biochemical technique—the analysis of tissue enzymes. Markert and his associates demonstrated electrophoretically that several enzymes existed as multiple molecular forms which they termed "isozymes". They showed that in some vertebrates, each species had its own characteristic pattern. Laufer, also at Johns Hopkins, demonstrated differences in esterase, malic and lactic dehydrogenase isozyme patterns in two species of silk worm moths and in their developmental stages as well.

Most of the previous electrophoretic studies of insect tissues have been confined to the use of body fluids for biochemical taxonomic characters. In the Hymenoptera, and particularly the bees, haemolymph is present in only trace amounts, insufficient for analysis. Muscle tissue of the thorax and femora is plentiful, and since muscle extracts of fish have proven to be comparatively species specific (1, 2) studies were initiated on these tissues in bees.

Analytical methods as outlined by Ornstein and Davis were employed with slight modification. Small-pore gel acrylamide (7%) was overlayed with a large-pore spacer gel (3%) and a large-pore sample gel containing the material to be analyzed. Buffer systems were composed of tris-glycine buffer at pH 8·3. Samples were run at $2\frac{1}{2}$ ma. per tube until the "front" had migrated an inch. General protein staining was done in 1% amido schwartz 10B and various substrate dye mixtures were used for enzyme staining.

Tissue was obtained from the thorax by laying it open and carefully excising only the homologous muscle from each of the species tested. This was extracted in 0·25M sucrose solution using a modified Potter-Elvehjem type tissue grinder, centrifuged at 9,000 × g for 10 minutes and using from 2 to 4 lambda of the supernatant for each tube.

Earlier paper electrophoretic studies on the haemolymph of *Periplaneta americana* revealed 2 to 4 distinct bands, whereas the same analysis conducted on polyacrylamide gel shows 14 or

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15 major reproducible fraction plus a number of fractions present in lesser quantity. Steinhauer (in litt.), through the use of two gel concentrations in the same tube, has found 22 constant reproducible fractions in blood of this species. The sensitivity of the technique is thus self-evident.

Preliminary studies of several species in different insect orders show remarkable quantitative and qualitative fraction differences. It is hazardous to generalize on the basis of the few specimens analyzed but in the more primitive orders there appears to be a quantitatively more protein of lower molecular weight than in the higher orders. At any rate the magnitude of ordinal difference in protein fractions is immense.

In the higher Hymenoptera (*Sphex*, *Andrena*, *Osmia*, *Megachile*, *Anthophora*, *Apis*, *Bombus* and *Psithyrus*) there is distinct generic specificity, with the major fractions occurring near the origin. The resemblances are evident, certainly when compared to pherograms of insects in other orders, but subordinal and familial groupings appear possible.

Comparisons of species within the subgenera *Pyrobombus* and *Fervidobombus* again reveal group differences, although as expected the magnitude of difference is not nearly as great as at the generic level.

A preliminary study on individuals of different populations of *Bombus huntii* indicates that pherogram configuration is slightly but consistently different in each of the geographically separated populations tested.

The esterase zymograms show differences of magnitude similar to that indicated above, but the number of analyses thus far conducted do not warrant any indications other than pattern trends. It is evident, however, that enzyme systems are useful biochemical substances in comparative taxonomy, a conclusion also reached by Tsuyuki (personal communication) among fishes.

If care is taken to negate or minimize the innate variability resulting from differences in age, sex, and technique it is clearly evident that there are numerous biochemical and histochemical techniques available to study phylogenetic relationships at the molecular level.

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HETEROGENEITY OF GLYCOLYTIC ENZYME PROTEINS IN INSECTS*

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The use of enzyme proteins as morphological traits was probably examined by Nuttall (1, 2, 3, 4, 5) in his early works, although he did not identify them as such. Analysis of tissues for enzyme heterogeneity has been done by Kaplan (6), *et. al.;* however the strict application of this technique to systematic entomology has not, to my knowledge, been accomplished (7). Thus this preliminary investigation seeks to establish that: (*a*) an enzyme heterogeneity exists that *is* species-specific; and (*b*) developmental changes in insects occur with corresponding changes in enzymes.

PREPARATION OF MATERIAL. A variety of insect thoracic muscle (frozen and used within 24 hours) was used for experimental work. The extraction solution consisted of a cold 0.1 molar Tris-HCl buffer at a pH of 7.2. It was centrifuged and filtered. A second centrifugation at 112,000 XG followed. The final step in enzyme preparation was dialysis of the ultracentrifuged supernatant against the extraction solution for 17 hours. Thus it was assured that the sample contained only soluble protein.

REAGENTS. Commercial preparations of NAD† and its analogs were utilized. All reductions of the cofactor were accomplished in the laboratory, using alcohol dehydrogenase. Yields were checked against molar absorbancy indexes for accuracy in determining final concentrations of the coenzyme. All other chemicals were of reagent grade.

MEASUREMENT. Enzyme reactions were followed spectrophotometrically utilizing the unique absorption properties of NAD and reduced NAD. Only the reduced form has a second absorption peak at 340 mu. Thus as oxidation of the coenzyme proceeds, the absorption is reduced. It was found empirically that reduced NAD followed Beer's Law and thus it was possible to plot the absolute molar fraction reacting against time. The stoichiometry of the reaction is one to one, therefore, the rate of substrate disappearance is known. The analogs of NAD behave in a similar fashion, although the second peak may occur at different wavelengths.

Kinetic studies were accomplished in a double beam spectrophotometer equipped with a water jacketed cell held at 30°C. Substrate was added to the sample cell at time zero. Results were plotted by means of a servo recorder attached to the spectrophotometer. Rate constants were determined directly from the graphs.

Protein determinations were based on spectral absorbancies of the dialysed enzyme preparation at 280 mu, using dialysed Bovine Serum Albumin as standard. In determining the accuracy of the method, the standards were checked for protein concentrations by a modified Lowry technique (8).

All kinetic data were reduced to common parameters by computing specific activities and by determining slope ratios. Work is in progress to determine the statistical significance of the findings.

As with chromatography and electrophoresis, the resolving power of this technique is limited, however, I feel confident that this will prove to be a powerful tool.

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†Abbreviations used: NAD—Nicotinamide adenine dinucleotide (DPN); APNAD—Acetylpyridine NAD; PANAD—Pyridine aldehyde NAD; TNAD—Thionicotinamide NAD; DENAD—Deamino NAD; APDENAD—Acetylpyridine deamino NAD; PADENAD—Pyridinealdehyde deamino NAD.

RESULTS. Two areas of information are currently under study. The first involves examination of developmental specificity of the enzymes and second, their species-specific nature. Since this area of research is new to entomology, the first tests were accomplished to determine whether an enzyme species specificity exists in populations of randomly selected taxa. The constancy of this species parameter has not yet been determined for varying conditions of environmental stress.

A. *Species Specificity:* In examining the data obtained from the species-specificity phase of this program, a number of tentative conclusions may be drawn. Table 1 presents some information of preliminary runs with a variety of insects as a guide to enzyme run reliability. Except for the termite workers, each of these figures represents the average of at least three different preparations of the same species. The passalid beetle preparations were tested for variation, and varied less than 3% in 15 separate trials of 4 separate preparations.

That differences exist between these species is clearly evident: however, no specific trends can be identified. These preliminary tests do indicate that an enzyme heterogeneity exists.

B. *Developmental Specificity:* For identification alone, it is essential that identical stages be examined, since salient points of morphological importance may be modified in different stages. Enzyme proteins as well, show changes during development, and thus their usefulness as taxonomic criteria is limited to the particular stage of the individual organism.

Following the same isolation procedures and kinetic techniques, a number of immature stages was examined for enzyme activity and compared with their adult counterparts. Table 2 portrays the results obtained with *Periplaneta americana.* There does appear a difference between the nymphal and adult forms. The double columns beneath each heading represent α-glycerophosphate dehydrogenase to the left and lactic acid dehydrogenase to the right. Table 3 represents *Blaberus craniifer* and *Magicicada septendecim.* Again these represent preliminary results, hence the trend is evident but a quantitative evaluation has yet to be made.

TABLE 1.

Activity slope ratios for glycerophosphate dehydrogenase from a number of insect species.

	NAD / APNAD	NAD / DENAD	NAD / PANAD	NAD / APDENAD	APNAD / DENAD	APNAD / PANAD	APNAD / APDENAD	DENAD / PANAD	DENAD / APDENAD
Orthoptera									
B. craniifer	·8	1·1	2·4	∞	1·4	2·5	∞	18·5	∞
P. americana	19·3	1·8	∞	93·3	·1	∞	4·8	∞	53·3
Gryllus sp.	∞	4·3	∞	∞	0	∞	0	∞	∞
Dissosteira carolinea (Thor)	20·0	2·0	∞	33·3	·1	∞	1·7	∞	28·3
Dissosteira carolinea (Fem)	∞	1·5	—	∞	0	—	0	—	0
Melanoplus femur-rubrum	∞	1·1	∞	∞	0	0	0	∞	∞
Homoptera									
Magicicada sp.	16·7	2·4	∞	—	·2	∞	—	∞	—
Isoptera									
Rhinotermes flavipes (Work)	∞	3·8	∞	36	0	∞	0	∞	9·5
Coleoptera									
Popilius disjunctus	65·5	1·5	87·3	40·9	·02	1·3	·6	60·3	28·3
Hymenoptera									
Apis mellifera (Drone)	13·2	1·4	∞	8·4	·01	∞	·6	∞	6·0
Apis mellifera (Worker)	∞	1·0	4·7	5·6	0	∞	0	4·7	7·1
Xylocopa virginica	10·0	1·2	∞	5·4	·1	∞	·5	∞	4·4
Vespa maculifrons	∞	1·6	95	34·6	0	∞	0	58·8	21·4

Table 2.

Slope ratios of *Periplaneta americana* dehydrogenases. The figure on the left hand of each column represents GPDH and on the right LDH.

	NAD TNAD		NAD APNAD		NAD DENAD		NAD APDENAD	
Adult	∞	2·2	8·8	∞	1·4	1·7	8·8	2·8
Nymph (late)	∞	∞	1·5	∞	∞	∞	∞	∞
Nymph (early)	∞	∞	1·5	1·0	∞	∞	∞	∞

Table 3.

Slope ratios of *Magicicada septendecim* (upper) and *Blaberus craniifer* (lower). See Table 2 for explanation of columns.

	NAD TNAD		NAD APNAD		NAD DENAD		NAD APDENAD		APNAD TNAD		APNAD APDENAD		DENAD TNAD		DENAD APDENAD		APDENAD TNAD	
Adult	4·6	·8	5·8	1·6	1·9	·8	55	·67	·8	·5	1·	·4	24	1·0	2·9	·8	·8	1·2
Nymph	∞	∞	18·	1·8	1·0	1·3	24·	2·2	∞	∞	1·3	1·2	∞	∞	24	1·8	∞	∞

	NAD APNAD		NAD DENAD		APNAD DENAD		APNAD PANAD		DENAD PANAD	
Adult	∞	0	·87	0	0	0	0	0	∞	∞
Nymph	2·5	1·0	·82	1·3	·3	1·3	14	∞	34	∞

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TAXONOMY OF PARASITIC AND PHYTOPHAGOUS INSECTS IN RELATION TO THEIR HOSTS

HOST RELATIONS IN THE CHALCIDOIDEA (HYMENOPTERA) AND THEIR TAXONOMIC SIGNIFICANCE

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Host specificity is rare among chalcids as also is a broad host range. Most species have a host range definable in terms of the systematic proximity of the hosts or of the host environment. For example, the host ranges of many of the chalcids attacking oak gall inhabitants are determined by the galls' form, position and season, and not by its contents. Host ranges of congeneric species may overlap, but they differ in points of emphasis. Host relations may be used therefore as a taxonomic tool.

Among British *Elachertus, E.olivaceus* (Thomson) attacks only *Coleophora* on rushes; *E.argissa* (Walker) may attack only *Coleophora* on trees. Leaf-mining Lepidoptera are parasitised by *E.florianus* (Walker), whilst larvae feeding in spun shoots or seed-heads of herbs and deciduous trees are parasitised by *E.nigritulus* (Zetterstedt). Until recently, *E.geniculatus* (Ratzeburg) was synonymised with *E.nigritulus,* but the host plant, a conifer, was a discordant element and examination of reared material revealed morphological differences between the two species.

A number of chalcids, e.g. *Eupelmus urozonus* Dalman and *Dibrachys cavus* (Walker), have large and diverse host ranges covering four or five insect orders. Species with wide host ranges should be critically examined. Perhaps the chalcid really is relatively indiscriminate in its choice of hosts, though all the hosts must share some feature, ecological or physiological, rendering them suitable. Or misidentification may have occurred, either of the chalcid or of the hosts. Initial misidentification of the chalcid is almost inevitable if an aggregate of sibling species is involved in which biological differences have outpaced morphological distinctions. *Eurytoma rosae* Nees was once thought to inhabit Cynipid galls on oak, rose, *Acer* and Compositae. Adults from different sources are indistinguishable on external morphology, but clear-cut differences exist in the eggs.

The picture of biologically distinct but morphologically similar species should be counterbalanced by our knowledge of intraspecific variation, especially when in response to different hosts. Males of *Trichogramma semblidis* (Aurivillius) reared from *Sialis* eggs differ from those from lepidopterous eggs in leg, wing and antennal structure. Such host-determined polymorphism is discoverable only by experimental breeding. Host size may influence parasite size, and the latter may be correlated with relative lengths of wing veins or antennal segments, or the strength and extent of sculpturation. These characters should therefore be used with discretion in separating species.

Colour is very variable in chalcids, specimens from warmer, drier climates generally being more lightly coloured. Seasonal dichroism is recorded in several species; usually the overwintering generation is darker than the summer generation. Seasonal dimorphism is less well known, but the ovipositor lengths of some *Torymus,* and the shape of the female gaster in *Olynx gallarum* (L.) differ in spring and summer generations. The two generations of this latter species, which have different hosts, were considered as distinct species until the life-cycle was understood.

It is evident then that biological data are of great importance in chalcid taxonomy, indicating the existence of sibling species or polymorphism, and also contributing towards our understanding of speciation and, possibly, phylogeny.

HOST SPECIFICITY OF FIG WASPS (HYMENOPTERA CHALCIDOIDEA, AGAONIDAE)

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For their procreation, fig wasps of the family Agaonidae are absolutely dependent upon plants of the genus *Ficus*, in whose gall-ovaries the larvae develop. The fig wasps serve the *Ficus* as pollinating agents. As one would imagine from the intimate, obligatory symbiosis, the fig wasps are specific to their hosts. Moreover, a comparison of the botanical and entomological classifications reveals the fact that related figs have related pollinating wasps. This phylogenetic specificity is illustrated by the following table, in which the sections of the genus *Ficus* are listed against the Agaonidae that act as their pollinators. Doubtful records are omitted from this list.

Ficus Linn.	Agaonidae
Urostigma (Gasp.) Miq.	
Urostigma	*Blastophaga* Grav.
Leucogyne Corn.	*Eupristina* Saund.
Conosycea (Miq.) Corn.	*Blastophaga* Grav., *Eupristina* Saund., *Waterstoniella* Gr.
Stilpnophyllum Endl.	*Blastophaga* Grav.
Malvanthera Corn.	*Pleistodontes* Saund.
Galoglychia (Gasp.) Endl.	*Agaon* Dalm., *Allotriozoon* Gr., *Elisabethiella* Gr.
Americana Miq.	*Julianella* Gr., *Valentinella* Gr.
Pharmacosycea Miq.	
Pharmacosycea	*Tetrapus* Mayr
Oreosycea (Miq.) Corn.	*Blastophaga* Grav.
Ficus	
Ficus	*Blastophaga* Grav., *Ceratosolen* Mayr
Sycidium Miq.	*Blastophaga* Grav., *Ceratosolen* Mayr
Rhizocladus Endl.	*Blastophaga* Grav.
Kalosyce (Miq.) Corn.	*Blastophaga* Grav.
Sinosycidium Corn.	
Adenosperma Corn.	
Neomorphe King	*Ceratosolen* Mayr
Sycocarpus Miq.	*Ceratosolen* Mayr
Sycomorus Miq.	*Ceratosolen* Mayr

Joseph (1, 2) recorded two species of Agaonidae from different trees of one and the same species of *Ficus* (*F. drupacea* Thunb.). As this is a strangling fig of the subsection *Conosycea*, the record of one of the wasps, *Eupristina belgaumensis* Jos., is in accordance with the principle of phylogenetic specificity. The other wasp, *Ceratosolen fusciceps* (Mayr), is known as the pollinator of *F. racemosa* Linn. (subgenus *Sycomorus*), which may have been the host tree of *F. drupacea!* I suggested as an obvious explanation of the double record that the intermingling twigs of host and strangling fig had confused the collector. A similar case is known in botany (Corner, 1960, in litt.): *F. clarkei* King is a mixture of *F. tinctoria* Forst. growing on *F. racemosa*. Joseph (1961, in litt.), however, denied this explanation in the case of *F. drupacea*, and maintained that one species of *Ficus* may be inhabited by two species of Agaonidae.

I have now examined a fig, which is actually inhabited by two species of Agaonidae. In the receptacles of *F. stupenda* Miq., collected in North Borneo by E. J. H. Corner, galls of *Ceratosolen* spec. and *Waterstoniella* spec. are situated side by side. As *F. stupenda* is, again, one of the strangling figs (and belonging to the same series as the host of another species of *Waterstoniella*), I assume the *Waterstoniella* to be the normal inhabitant. The species of *Ceratosolen* probably will prove to be the normal pollinator of the host tree.

The now unambiguously established fact that two species of fig wasps can reproduce in the receptacles of the same fig, should warn against too much generalization of the host specificity principle. The phylogenetic specificity found in the instances mentioned above, however,

once more infers the correctness of the assumption that figs and fig wasps have evolved together, and that, notwithstanding some exceptions, host specificity is the rule.

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LIFE HISTORY STUDIES IN CHALCIDOID (HYM.) TAXONOMY

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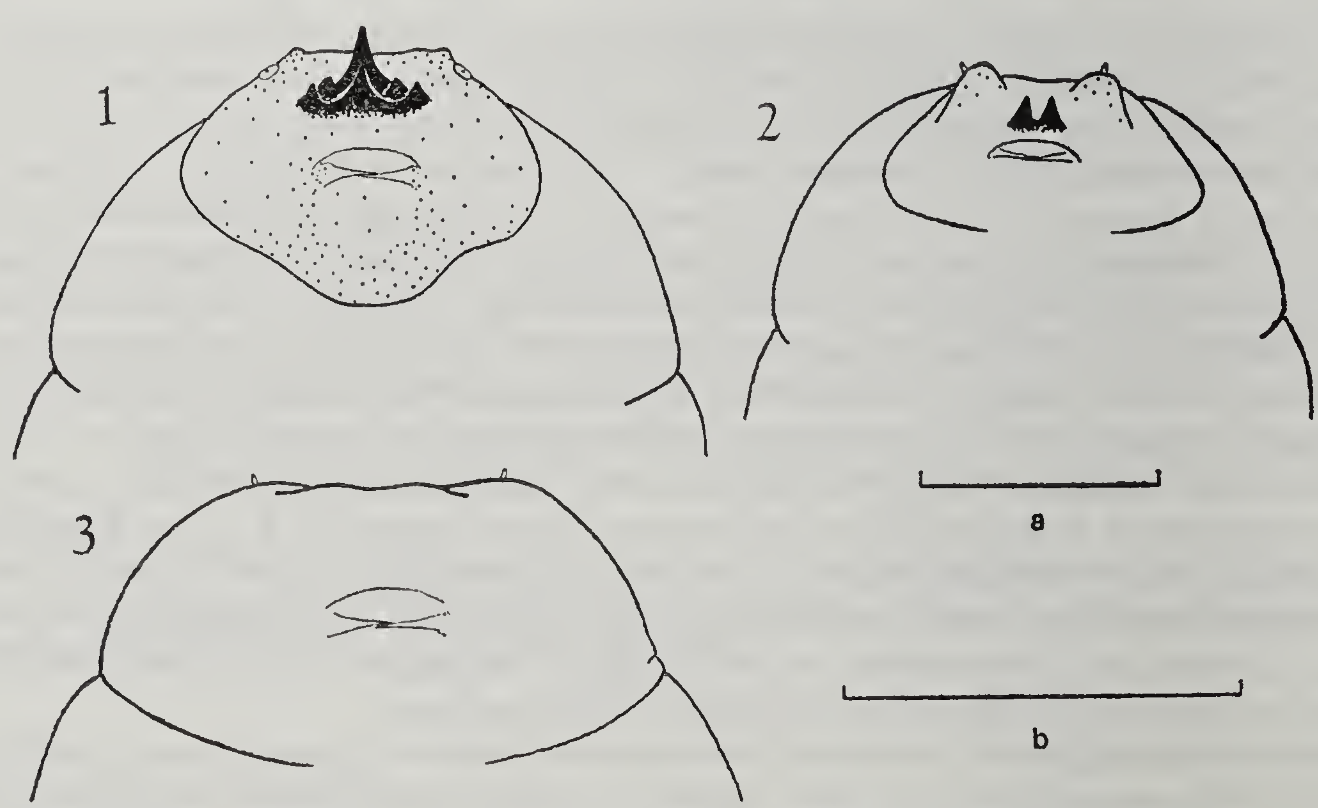
Intensive systematic work on the Chalcidoidea during the last ten years or so, culminating in the publication of a key to European genera (2), has opened the way to comparative ecological and biological studies. It is not surprising that in turn such studies have important contributions to make to taxonomy. There can now be little doubt that in most insect groups with specialised larval feeding habits species discrimination relying solely on morphological studies will not be adequate for either the field biologist or the economic entomologist.

The kind of biological information most obviously of use to the taxonomist is to be derived from life history studies including morphological details of eggs, larvae and pupae. Preliminary investigations on the species allied to *Eurytoma rosae* Nees (Eurytomidae) have shown remarkably obvious differences in sculpturing and pattern of egg shells, apparently correlated with distinct host preferences (1). Such obvious differences occur between species as yet inseparable when adult material alone is available. Recent investigations suggest that the very closely allied *E.curculionum* Mayr has an even more distinctive egg.

The species of the Pteromalid genera *Chlorocytus* Graham and *Stenomalina* Ghesquière (=*Stenomalus* Thomson) are clearly very closely allied. All the known species attack stem-feeding larvae and many appear to be endophagous. *Stenomalina* species, where known, attack dipterous larvae, mostly Chloropidae in grasses (Gramineae). *Chlorocytus* species



Figs. 1-3. Heads of larvae of Chalcidoidea.

attack a wide range of hosts including Cephids (Hym., Symphyta) and *Tetramesa* species (Hym., Eurytomidae) in grasses, and *Melanagromyza* species (Dipt., Agromyzidae) and Cynipids (Hym., Cynipoidea) in various herbaceous plants. The larvae of both genera are characterised by the possession of protuberances on the head above the clypeal area. In *Stenomalina* these are heavily sclerotised and form a characteristic pattern (fig. 1), which is highly variable in detail even between individuals of one species. In *Chlorocytus* the protuberances, which show little intraspecific variation, are represented as a pair of simple processes arranged side by side. They may be very obvious and sclerotised in some species (fig. 2), or only slightly developed and unsclerotised in others (fig. 3). Thus, so far as known, larval anatomy at least does not contradict the taxonomic division of the group into two genera. Species discrimination particularly in *Chlorocytus* is often extremely difficult. Large scale rearings from grasses suggest that a number of species closely allied to *C.pulchripes* (Walker) must be recognised, each with distinct host and plant preferences. Ultimately detailed field sampling and experimental breeding will be necessary to solve the problems of species discrimination in many Chalcidoid genera.

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THE PTEROMALID PARASITES (HYM. CHALCIDOIDEA) OF CERTAIN TRYPETID LARVAE (DIPT.)

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The larvae of Trypetidae are all phytophagous, sometimes inducing gall formation. Chalcids attack many of these larvae, but the precise interrelationships, especially those of the Pteromalidae, have been largely speculative.

The Trypetid larvae studied may be classified into three ecological groups:

1. *Urophora* species which are found in hard woody galls in flower-heads and stems of certain *Cynareae* (the thistle group of the Compositae). The larvae feed in vertical flask-shaped chambers which have their necks open to the exterior.

2. Several genera and species which feed in flower-heads of various Composites, mostly Cynareae, larvae in or near the capitulum leaving little external sign of their presence.

3. Three species: (*a*) *Ditricha guttularis* (Meigen), larvae in galls at base of stem of *Achillea millefolium* L.; (*b*) *Oxyna parietina* (L.), larvae in cells in stems of *Artemisia vulgaris* L.; (*c*) *Paroxyna misella* (Loew), larvae also in *Artemisia vulgaris* L., Summer generation in galls at stem apex, Autumn generation in flower heads.

The gall-forming species of *Urophora* are all attacked by *Habrocytus elevatus* (Walker). The female inserts the ovipositor into the neck of the flask-shaped chamber and paralyses the host. The egg is laid on the surface of the host and the larva which hatches feeds as an ectoparasite.

Habrocytus albipennis (Walker) parasitises the non-gall-forming flower-head feeders by pushing the ovipositor through the side of an unopened flower-head and laying the egg inside the host. The host continues to feed normally until the puparium is formed. At this stage the parasitic larva feeds very rapidly and pupates. The adult finally emerges by biting its way out of the puparium. *Habrocytus musaeus* (Nees) *trypetae* Thoms. is ectoparasitic on only two species of this group of Trypetids, *viz. Terellia longicauda* (Meigen) and *T.serratulae* (L.), and appears to attack no other host.

The three Trypetid species which feed in stems are each attacked by one or more specific Pteromalid parasites.

The host ranges of *H.elevatus* and *H.albipennis* are therefore considerably wider than those of the other Pteromalids. They appear to search Composites, mostly Cynareae, for their hosts. *H.elevatus* is specific to the gall-forming species of *Urophora*, whilst *H.albipennis* oviposits in the non-gall-forming flower-head feeders. Some of the other species of *Habrocytus*, here

stated to be specific, may have wider host ranges than is apparent at the moment. But this is unlikely in the case of those attacking stem feeding larvae, as they have very specialised feeding habits.

As *H.elevatus* and *H.albipennis* have such wide host ranges, the possibility that they represent two groups of very closely allied sibling species must be considered. This would seem more likely in the case of *H.elevatus* as it attacks larvae in both flower-head and stem galls. *H.albipennis* is a very variable species morphologically, but as yet no characters which can be consistently correlated with any particular host record have been seen.

THE CLASSIFICATION OF BRACONIDAE (HYM.) IN RELATION TO HOST SPECIFICITY

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In this paper I would like to collate the present system of Braconidae (cf. Muesebeck, Catalogue of North American Hymenoptera) with the available knowledge of their biology and larval taxonomy and then to discuss the position of some genera in higher groups that do not fit in biologically. In conclusion a phylogenetic scheme of Braconidae (fig. 1) is suggested.

The subfamily Euphorinae resembles bionomically Aphidiinae as all its genera except *Meteorus* live endoparasitically in adult insects of various orders. *Meteorus* parasitizes larvae of Lepidoptera or Coleoptera internally, but the larval characters differ from those of all other genera of Euphorinae throwing doubt on its correct placing here. The subfamily Helconinae has four tribes: the first three of them, Cenocoeliini, Helconini, and Diospilini, parasitize the larvae of woodboring Coleoptera internally and the larvae are uniform taxonomically. *Meteoridea* Ashm. (Diospilini) appears wrongly placed because it is an internal parasite of lepidopterous larvae and pupates inside the host pupa, and its larval morphology differs *Meteorus* live endoparasitically in adult insects of various orders. *Meteorus* parasitizes larvae strikingly from that of other Helconinae. It seems to form a transition between Cyclostomi and more progressive groups of Braconidae. The representatives of the fourth tribe, Zelini, are parasitic in larvae of Lepidoptera too, but their larvae resemble more closely those of Macrocentrinae than of Helconinae. The Blacinae represent a very unnatural and heterogeneous group on a basis of both their bionomics and larval taxonomy. The first group of genera, *Blacus* Ns., *Calyptus* Hal., *Urosigalphus* Ashm., *Aliolus* Say, and *Triaspis* Hal., are internal parasites of coleopterous larvae and are also a distinct group in the larval stage. The second group, *Syrrhizus* Foerst., *Centistes* Hal., and *Pygostolus* Hal., parasitize adults of Coleoptera and on a basis of larval morphology should be more closely related to Euphorinae than to Helconinae. The genus *Eubadizon* Ns. is an internal parasite of lepidopterous larvae and on the basis of larvae it should be connected with Macrocentrinae. The last group of genera of Blacinae, *Orgilus* Hal., *Microtypus* Ratz., and *Stantonia* Ashm., are also internal parasites of larvae of Lepidoptera. They form a natural transition to the next subfamily, Agathidinae.

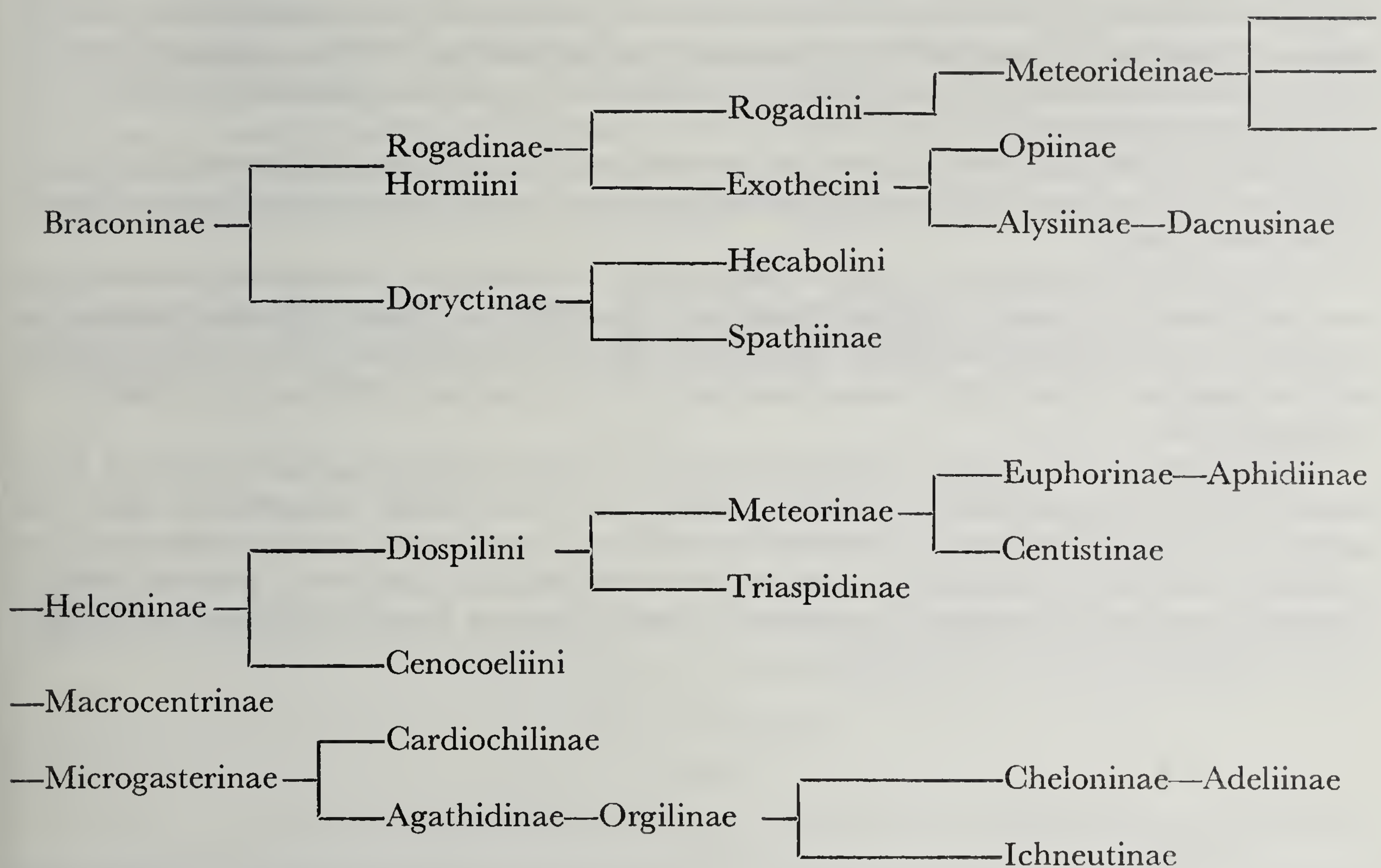
The large subfamily Microgasterinae is biologically homogeneous—the species are endoparasites of lepidopterous larvae. Using larval taxonomy, two distinct groups of genera can be easily distinguished: (1) the typical Microgasterinae; (2) the genera *Mirax* Hal., *Adelius* Hal., *Dirrhope* Foerst., and *Paroligoneurus* Mues. forming a special group closer to Cheloninae than to Microgasterinae. The species of Cheloninae have very specialised habits: they lay their eggs in the host eggs, but the parasitic larvae do not become mature until the host larvae have reached maturity. The Ichneutinae have probably the same habits and it seems probable that the Adeliinae too, because these groups have very similar larvae.

The members of the next three subfamilies, Dacnusinae, Alysiinae and Opiinae, are endoparasites of Diptera. The genus *Gnaptodon* Hal. does not fit in this group either biologically or on larval morphology, and it seems wrongly placed in Opiinae. It resembles Exothecini.

The cyclostomine division is probably the most primitive and includes those whose females paralyse the host larvae before egg-laying and whose larvae develop externally on the paralysed host. The tribe *Rogadini* seems to be a little heterogeneous from the biological aspect, but otherwise it is the most specialised group of Cyclostomi. Finally, the Cosmophorinae cannot

be a cyclostomine group as its members are internal parasites of adult bark beetles and their larvae resemble those of *Centistes* Hal. and *Syrrhizus* Foerst. from Blacinae.

I consider the Braconidae a specialised group that developed from Ichneumonidae. They are probably monophyletic and can be placed in a system as shown below:



LA CIMICOPHAGIE DES *CATHAROSIINI* ET L'INCLUSION DE CETTE TRIBU PARMI LES *PHASIINAE* (*DIPTERA LARVAEVORIDAE*)

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Décreétée, plus ou moins empiriquement, sur la base de caractères morphologiques classiques, la position taxinomique du genre *Catharosia* Rond. et de ses alliés demeure encore controversée.

Certains Diptéristes (Townsend à partir de 1936; Rubtzov 1951; Verbeke 1962 . . .) les tiennent pour des *Phasiinae* s. str., notion qui coïncide étroitement avec celle de Tachinaires cimicophages (cf. mon "Essai monographique sur les *Phasiinae*" in Mém. Mus. nat. Hist. nat., Zool., t.26, 1963).

Cependant, depuis Brauer et Bergenstamm (1891), qui hésitèrent à placer *Catharosia* dans les "Anurogynen" ou dans les "*Phytoidae*", d'autres auteurs considèrent toujours les *Catharosiini* comme des Tachinaires parasites de Coléoptères adultes (*Dufouriinae*) (Stein 1924; Mesnil 1939, 1950) ou comme des *Rhinophoridae* (Villeneuve 1924; Lundbeck 1927; Belanovsky 1951); ils les excluent ainsi, respectivement, des *Phasiinae* ou des Tachinaires.

Ces divergences d'opinions ressortissent, avant tout, au peu de signification des caractères morphologiques imaginaux généralement invoqués pour la classification des Diptères supérieurs.

Tout en soulignant, dans l'Essai précité, la faiblesse intrinsèque des systèmes correspondants, j'ai cependant suivi, dans le cas particulier, l'avis de Mesnil et écarté les *Catharosiini* des *Phasiinae;* en l'absence de toute donnée plus significative concernant cette tribu, il eût été

plus conforme à ma propre méthode de l'étudier pour mémoire avec les autres taxa, tout aussi *incertae sedis*, rapprochés à divers titres des *Phasiinae*.

Les faits que j'ai établis récemment, à la Station de Parasitologie de Richelieu (Indre et Loire), me permettent de réparer cette omission et d'en tirer certaines conclusions méthodologiques.

Grâce à l'élevage de *Catharosia pygmaea* (Fall.) à partir d'imagos de *Beosus maritimus* (F.) (*Heteroptera*, *Lygaeidae*), je puis, en effet, préciser que les larves de cette mouche sont cimicophages, présentent aux trois stades tous les caractères de celles des *Phasiinae*, vivent en parasites solitaires dans la cavité générale de l'hôte et y induisent un siphon respiratoire secondaire fixé à une trachée thoracique.

Ce sont là les caractères larvaires et "parasitiques" les plus significatifs des *Phasiinae*, et l'on ne peut plus douter de l'appartenance des *Catharosiini*—ou plus exactement du genre type—à cette sous-famille.

Sur un plan plus général, étant donné la valeur discutable des caractères traditionnellement appliqués à la classification des Tachinaires, il semble que, jusqu'à preuves décisives du contraire, les décisions taxinomiques fondées sur ces seuls caractères—et de quelqu'autorité qu'elles émanent—doivent être tenues pour purement indicatives et également probables . . . ou improbables.

En conséquence, les cadres supratribaux de Tachinaires doivent demeurer ouverts à toute introduction que justifierait les données biologiques. Ceci oblige, notamment, dans tout système ou révision, à mentionner comme tels *tous* les taxa *incertae sedis* (souvent subtypiques ou atypiques au sens de Townsend), en annexe provisoire aux taxa typiques de position connue; l'ouvrage y perdra une certaine beauté factice, mais y gagnera quant à sa valeur en tant qu'outil d'information et de recherche.

HOSTPLANT RELATIONSHIP AS A TAXONOMIC CHARACTER IN SAWFLIES (HYMENOPTERA, SYMPHYTA)

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Ecologically one of the most important single factors in Flowering Plants is whether they produce secondary wood or not, whether they make closed forests or open habitats for animals to live in. Hutchinson (3) stresses this as a basic dichotomy in their phylogeny.

This ecological dichotomy is evidently fundamental in sawfly foodplant associations (1 and 2). The most primitive families, Xyelidae, Pamphiliidae, Syntexidae, Xiphydriidae, Siricidae and Orussidae are entirely associated with arborescent plant-families, (though the Orussidae are actually parasites, but parasites of wood-boring Coleopterous and other larvae) and only the Megalodontidae and Cephidae feed partly on herbaceous plants.

In the Tenthredinoidea the more generalised families, the Diprionidae, Pergidae, Argidae and Cimbicidae are also almost entirely associated with arborescent plants though the Blasticotomidae are on herbaceous plants (Filicales), but the Tenthredinidae themselves are divided between arborescent and herbaceous plants.

In these more primitive sawfly families on arborescent plants a number of genera occur on Coniferae, but no known genus has species on Coniferae as well as species on Angiosperm trees. And when in any group some genera are on Coniferae and some on Angiosperms, those on Coniferae are the most primitive in structure (except possible in Xyelidae). This applies to the Siricidae (Siricinae on Coniferae and Tremecinae on Angiosperms), Pamphiliidae (Cephalciinae on Coniferae and Pamphiliinae on Angiosperms) and Argidae (Zenarginae on Coniferae in Australia, Arginae and Sterictiphorinae on Angiosperms).

In the Cephidae the Hartigiini, attached to arborescent families, are more generalised than the Cephini attached to Gramineae. In the north temperate zone there is a frequent association between the Rosaceae and the catkin-bearing families Betulaceae, Corylaceae, Fagaceae

and Salicaceae as sawfly host-plants. This may be no more than simple association with trees rather than herbs, because most of the north temperate angiosperm trees are either rosaceous or catkin-bearing, but Hutchinson derives these catkin-bearing trees from rosaceous ancestors.

In the Tenthredinidae, however, two of the four subfamilies, the Selandriinae and the Tenthredininae, are predominantly on herbs, many of the Selandriinae on Filicales. In this family there are also several genera on Ranunculaceae closely related to genera on Monocotyledons such as Liliaceae, Gramineae and Cyperaceae; Hutchinson (3) also associates these groups phylogenetically by deriving Monocotyledons from Ranunculous ancestors.

The fact that coniferous trees are associated with angiosperm trees and angiosperm herbs with ferns as sawfly foodplants does point to the association being ecological rather than phylogenetic. Plant phylogeny is only relevant here because the more closely plants are related the more similar they are likely to be physiologically.

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THE SPECIES-HOST RELATIONSHIP IN THE AGROMYZIDAE (DIPTERA) AS AN AID TO TAXONOMY

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The major advance in clarifying this family was achieved by Hendel, as a direct result of combining his taxonomic work with a study of host-plants.

The study of the biology of the Agromyzidae led to a considerable advance in our knowledge of the family but the attachment of too great a degree of importance to the food-plant had its dangers from the taxonomic point of view. The pendulum was beginning to swing too far and it became assumed that because a fly had been discovered for the first time on a new plant family or genus, then *ipso facto* it must represent a new species. Many taxonomic errors resulted, directly attributable to this general attitude.

The table below analyses the species in the Ethiopian, Oriental, Australian and Neotropical Regions, showing first, the number of known species, second, the number which have been bred and for which the host-plant is known and these have been further broken down into those which are monophagous, oligophagous and polyphagous.

Region	*Known species*	*Number with known host-plant*	*Monophagous*	*Oligophagous*	*Polyphagous*
Ethiopian	213	86	71	13	2
Oriental	113	46	25	18	3
Australian	57	32	22	8	2
Neotropical	152	67	51	11	5

It is apparent from this table that a high proportion of species in all regions are monophagous, with a substantially smaller number being oligophagous. Equally striking is the very small number of species which are truly polyphagous.

Among leaf-miners the majority of monophagous species are not limited to a single host but occur on a number of species within a genus. Strict monophagy does occur among leaf-miners but rather infrequently. Numerous species are not leaf-miners but feed on other parts of the plants, such as stems, seeds or as gall-causers or in one unusual case as a feeder on young thorns on acacia. There is a high degree of probability that such species will be strictly monophagous. Where the feeding habit suggests strict monophagy, one can be reasonably certain that the species is distinct and this is a valuable guide to its taxonomic status,

The truly polyphagous species as my table shows are extremely few. Interesting examples are the leaf-mining species *Liriomyza sorosis* (Williston) and *L. trifolii* (Burgess) from Florida, *Melanagromyza passiflorae* Hering in the Ethiopian region and *M. atomella* (Malloch) in the Oriental and Australian regions. There is only one known case of a polyphagous stem-borer—*Melanagromyza virens* (Loew), described from North America.

The first breakthrough in the study of the Agromyzidae came from the realisation that a high proportion of species were monophagous or at least oligophagous. During the past few years a second, comparable breakthrough has been achieved, based on the study of male genitalia. In view of the extraordinary diversity and constancy of male genitalia in the Agromyzidae, reliance on the host association as an aid to taxonomy has now become of secondary importance.

In conclusion, I would like briefly to summarize my own experience with the species-host relationship in the Agromyzidae as follows:—

1. Where the topospecificity of a species is unusual, there is little doubt that the species will be strictly monophagous, and any such new case coming to light can be confidently assumed to represent a new species.
2. Seed-feeders and stem-borers are normally either oligophagous or more frequently monophagous.
3. The majority of leaf mining species will prove to be monophagous within a genus or more frequently oligophagous.
4. True polyphagy is rare and few, if any, further cases are likely to be found.

BIOSYSTEMATICS OF AMERICAN *PEMPHIGUS* (HOMOPTERA: APHIDOIDEA)

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It is obvious that aphids of the genus *Pemphigus* have been associated with *Populus* spp. for a long time. The Salicaceae are an ancient group of plants even though now they are quite specialized. The genus *Populus* (30-40 species) is the primitive genus in the group. The fact that they hybridize readily means that many clonal groups occur and often the aphids associated with these clones may exhibit a range from complete resistance (*Pemphigus bursarius*) to distinctive gall formations (*Pemphigus populivenae*). The fact that many trees in this group reproduce by sending out underground roots means that there are often congregations of distinctive hybrids arising originally from a single tree.

From the world point of view the black poplar group (*nigra*, *deltoides*, *berolinensis*, *canadensis*, *sargentii*, *fremontii*, *maximowiczii*) has about 20 species of the total number of *Pemphigus* species associated with it of which about 80 per cent occur only on this group. The balsam group of *Populus* spp. (*balsamifera*, *acuminata*, *angustifolia*, *trichocarpa*) account for 10 species of which 50 per cent do not cross-over to other poplars. The white poplars (*tremuloides*, *alba*, *grandidentata*) have only a few species associated with them and most go to other groups of poplars. The section Turunga includes poplars with polymorphic concolor leaves (*euphratica*) and only one species (*lichtensteini*) is associated with it and it goes to black poplars.

From a world point of view there seems to be little evidence of the selection of particular families of plants in connection with their asexual cycles. At least 18 families of plants are recorded with the greatest number (11) recorded from the roots of Compositae.

The American species of *Pemphigus* can be associated with their primary hosts based on groupings of poplar (Table 1). There is some cross-over with *Pemphigus populicaulis* and *P. populitransversus* (species in parentheses) but in general the two main groups are those associated with the balsam poplars and those associated with the black poplars. The white poplars usually occur at higher elevations and the short season available for a life history makes it difficult for *Pemphigus* spp. to persist.

Many American species of *Pemphigus* are known from only viviparae on the roots of the secondary hosts. *P. auriculae* is represented only by two slides in the Essig collection at Berkeley, California. Two known species of *Pemphigus*-like aphids occur on the roots of *Salix* in

California—one from northern California and one from southern California. Sexuparae are known of these species and several eggs have been obtained from the species in the north. Morphologically they are quite distinct. These species undoubtedly belong to the same group as two already described species—*P. salicicola* H.R.L. from Greenland, and *Parathecabius salici-radicis* Börner from the East Alps. The species in northern California feeds on rootlets of *Salix* growing along streams and colonizes on the roots for a limited period in the summer and fall—indicating that another host is involved. The southern California species, on the other hand, occurs all year around on the roots of *Salix*, and is spread by the first instar nymphs which are equipped with waxy filaments for wind dispersal.

The primary host relationships are not known for *P. brevicornis*, *tartareus*, or *ephemeratus* which occur in Illinois on the roots of *Erigeron* (or *Solidago*), *Bidens*, and *Betula* respectively. In California we have viviparae on the roots of *Baccharis* (Compositae), *Euphorbia*, *Solidago*, *Juncus* and grasses. It will take much biological work to associate these species. There is no evidence for some of them, such as the species on the roots of *Baccharis*, that a primary host is involved. This species often spends an entire year on the roots without the formation of alates.

TABLE 1.

Recorded hosts of American *Pemphigus*, arranged by *Populus* group

Species	*Primary Host*	*Secondary Host*
	Balsam Poplar Group	
balsamiferae	*angustifolia*, *balsamifera*, *trichocarpa*	*Beta*, *Chenopodium*
monophagus	*angustifolia*, *balsamifera*	
populiglobuli	*angustifolia*, *balsamifera*, *trichocarpa*	
populivenae (=*betae?*)	*angustifolia*, *balsamifera*, *trichocarpa*	*Beta*, *Chenopodium*, *Spinacia*, *Amaranthus*, *Rumex*
populicaulis	*balsamifera*, *trichocarpa*, *acuminata*, (*sargentii*)	*Oenanthe*
	Black Poplar Group	
bursarius	*nigra italica*	*Lactuca*, *Sonchus*, *Xanthium*, Compositae
junctisensoriatus	*deltoides*, *sargentii*, *fremontii*	—
nortoni	*fremontii*, *sargentii*	—
populiramulorum	*fremontii*, *sargentii*	—
populitransversus	*fremontii*, *sargentii*, (*deltoides*), (*angustifolia*) *canadensis*	Cruciferae
	White Poplar Group	
populitransversus	(*tremuloides*)	Cruciferae

The lack of information on secondary hosts for known species forming galls is readily apparent in referring to Table 1. We have associated only three species in California over a period of several years with their hosts. Grigarick and Lange (1) found that the sugar beet root aphid in California is definitely what we have been calling *P. populivenae* Fitch. Typical galls were produced on *Populus trichocarpa* and secondary hosts included *Beta vulgaris* (sugar beets and Swiss chard), *Spinacia oleracea*, *Chenopodium album*, and *Amaranthus graecizans*. Later experiments indicated that a strain from *Rumex crispus* also, but with some difficulty, produced typical *populivenae* galls on *Populus trichocarpa*. The taxonomic status of *Pemphigus betae* Doane is dubious but in our estimation it would refer to *populivenae* and not *balsamiferae*. *P.balsamiferae* is easily separated from typical *populivenae*, but intermediates between the two occur in Washington state and in the White Mountains of California. Undoubtedly *populivenae*, *betae* and *balsamiferae* are part of the same complex. *P. balsamiferae* seems to be more of a Great Basin type entering California and Washington in more arid areas.

There is also some evidence of strains within the *populivenae* complex based upon numbers of caudal hairs. This evidence and certain differences in the life histories of particular strains indicate a degree of variance which will require more detailed investigations.

One species, *P. monophagus*, has been found in California to spend its entire life history on *Populus trichocarpa*. Eggs are deposited under the bark of the old dead twigs.

The life history of *Pemphigus bursarius* is similar to that in Europe. Damage to lettuce has occurred in Maine, Montana, Washington State, California, and perhaps other localities. The details are given in the article by Lange (2). In *bursarius* the primary host is necessary as it is unusual for this species to carry through winter on the secondary hosts.

One species, *P. populitransversus* over-summers in the egg stage in California. Alates fly to *Populus fremontii* (California) in May and galls are produced on the new roots of cruciferous plants.

Although experiments have been conducted with some of the other species we still have no idea of the host relationships of *Pemphigus populiglobuli, populicaulis, junctisensoriatus, nortoni* and *populiramulorum*.

In *P. populiramulorum* we have a species that apparently produces two kinds of galls on the primary host depending upon whether the gall is placed on the new wood or on the leaf petiole. All of our California material seems to be the leaf petiole form which appears superficially to be of the *bursarius* type.

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THE NEARCTIC SPECIES OF THE GENUS *IDIOCERUS* (HOMOPTERA) IN RELATION TO THEIR HOST PLANTS

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This paper is a brief summary of data obtained whilst revising the Nearctic species and is our present knowledge of the host plant relationship of this group of leaf hoppers.

The term "host plant" is used to include both the true host plant, in which eggs are deposited and on which nymphs develop, and the food plant that the adults use as a source of food. In general, the host plant and the food plant of *Idiocerus* species are suspected to be the same plant. Much of the data was obtained by the sweep method, but species were reared and observations were made in the field to verify as many records as possible.

In the Holarctic region most species of *Idiocerus* have as their primary host plants either willows (*Salix* spp.) or poplars (*Populus* spp.). In the Nearctic region 33 of the 52 known species occur on these host plants, and it is suspected that 7 other species in which the host plant is unknown, will also belong to this group. This means that approximately 4/5 of the species in the Nearctic region have as their host plants either poplars or willows.

Only 4 of the Nearctic species occur on both poplars and willows. These same species have been considered, by genitalic and other morphological characters, to be species from which many other species have evolved.

It is also interesting to note that 6 of the species occurring on willows and poplars have adapted to species of plants outside the family Salicaceae. These 6 are known to occur mainly on the members of the family Pinaceae. There are however, 2 other species, *I. apache* and *I. taxodium* which occur only on junipers and cypress respectively. These two are very closely related to the other species occurring on Pinaceae and have undoubtedly evolved from this group.

Three other species, *I. ensiger, I. tahotus,* and *I. morosus,* are only found on currants (*Ribes* spp.) and it is believed that these were also descended from the willow and poplar group.

The remaining six species of Nearctic *Idiocerus* live on various plants but none of these species have ever been found on willows and poplars. This group of species is also separate by

genitalia as well as other morphological characters. Two of the species, *I. provancheri* and *I. fitchi*, are very closely related to two Palaearctic species, *I. notatus* and *I. pruni* which are also genitalically different from the remaining Palaearctic species. The other four species occur only in the Southwestern part of the United States and Mexico and are seemingly indigenous to that area. These seemingly occur on oaks (*Quercus* spp.) and sumacs (*Rhus* spp.).

The following list summarizes the host plant data as they stand at the present time:

Number of Idiocerus Species Occurring on Host Plants

		Nearctic	*Palaearctic**
Pinaceae:	Picea	1	
	Sequoia	3	
	Taxodium	1	
	Juniperus	5	
Salicaceae:	Populus	18	16
	Salix	19	15
Corylaceae (Betulaceae):	Betula		1
	Alnus	1	3
Fagaceae:	Quercus	1	
Ulmaceae:	Ulmus	2	
Saxifragaceae:	Ribes	3	
Platanaceae:	Platanus		1
Rosaceae:	Pyrus (Malus)	2	
	Crataegus	3	
	Prunus		2
Anacardiaceae:	Rhus	1	
Aceraceae:	Acer		3
Tiliaceae:	Tilia		1
Unknown		10	

*From Ribaut, H. 1952. Faune de France.

EFFECT OF TEMPERATURE WITH AND WITHOUT HOSTS ON FOUR FIELD BIOTYPES OF CORN LEAF APHID, *RHOPALOSIPHUM MAIDIS* (FITCH)

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Hosts evaluated were Reno, Spartan and Kentucky I barley, Clintland and Dodge oats, Comanche wheat and Piper Sudan 428-1. Tests were conducted at constant temperatures of 45, 55, 65, 75, 85 and 90°F. Information on hosts and temperatures summarized here was presented by Singh and Painter (1964). (2).

Differential longevity of the four biotypes in absence of host plants at three constant temperatures of 60, 70 and 80°F. was also evaluated.

Materials and Methods. Origin of the four biotypes has been indicated by Painter and Pathak (1). Experiments were conducted in a Percival walk-in plant growth chamber at constant light intensity of approximately 1,500 foot candles 16 hours daily. For the progeny test, plants were grown in 4½-inch earthen pots. Five last instar nymphs of alate aphids were confined on a leaf of each variety by a transparent ventilated plastic box. Final counts of aphids were made 10 days after they were caged.

Alate adult aphids that had developed wings within the previous 24 hours were used in studies of comparative longevity of biotypes in absence of food. Each was confined in a separate plastic box. Humidity always was near saturation point inside and around the cages. Number of living aphids was recorded every half hour until the last one died.

Results and Discussion. Biotypes were unlike in raction to differences in temperature, and change of host brought significant changes in rate of reproduction.

Optimum reproduction for the four biotypes on Reno and Spartan barley was at 75°F. Optimum temperature ranged from 55°F. to 75°F. for the other five hosts, indicating that temperature effects usually are markedly influenced also by host. On Kentucky I optimum for four biotypes was 65°F. except for KS-2 whose optimum was 75°F. The optimum for four biotypes on Clintland and Dodge oats was 65°F.; Comanche wheat, it was 75°F. for KS-1 and KS-2, but 65°F. for KS-3 and KS-4, and 55°F. for KS-1, KS-3 and KS-4 on Piper Sudan 428-1. On Piper Sudan 428-1 optimum for KS-2 was between 55 and 65°F.

The most favourable temperature for distinguishing biotypes on different host plants was 75°F. especially on Reno barley and Comanche wheat, on which all biotypes differed significantly. KS-4 often had higher fecundity at lower, and usually also at higher, temperatures than other biotypes, especially on barley. At 90°F. only KS-2 survived on Reno and Kentucky I barley, and then the few young produced died within ten days, although a few parents lived the full 10 days.

Significant and nonsignificant differences in longevity of starved individuals among biotypes were found at the three constant temperatures. Survival time for KS-1 was significantly greater than for KS-2 and KS-3 at all three temperatures. KS-1 did not differ significantly from KS-4 at 70°F., but did at 60 and 80°F. KS-2 and KS-3 did not differ significantly at 60 and 70°F. but were highly significantly different at 80°F. KS-2 and KS-3 longevity was significantly shorter than it was for KS-4 at all three temperatures. Biotypes reacted more alike at 70°F. than at 60 or 80°F. KS-4 survived longest at 60°F. followed by KS-1. KS-2 had the shortest survival time at 80°F. and generally lived a shorter time.

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THE PROCESS OF ORIGIN OF A NEW FORM AT SPECIFIC LEVEL IN *DYSAPHIS* BÖRNER, THROUGH ADAPTATION TO A NEW HOST PLANT

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The study of the processes of speciation is very important for different fields of biology as much from a theoretical as from a practical point of view. Aphids with their high development rate can serve as a good subject for such investigations.

In 1957 in the Northern Caucasus the following experiment was carried out. A number of offspring of an initial individual of *Dysaphis anthrisci majkopica* Shaposhnikov were bred on its normal host (*Anthriscus nemorosa*) during many generations; these constituted the control (M). Another part of the offspring of the same initial individual was reared on a relatively unsuitable plant, *Chaerophyllum bulbosum.* Following intensive natural selection the aphids became entirely adapted to the new plant by the ninth generation. Some other identical experiments gave quite the same results (1).

During the process of adaptation the amplitude of variability increased in each successive generation of aphids, and their morphology gradually changed. In the eighth generation the variability reached its greatest value. Thus, in the experimental population the mean standard deviation (σ) and coefficient of variation (C) for a number of characters were 2-3 times as high as those in the control population. The sphere of action of natural selection was thereby enlarged.

From the eighth to the ninth generation the larval mortality fell from 56% to 7%, and the sharpest changes in morphology took place. At the same period the aphids lost the ability to feed on their former host (*Anthriscus*) and acquired the ability to live and reproduce on *Chaerophyllum maculatum*, which was formerly quite resistant. Thus a *new form* of aphid (N)

appeared. This new form acquired statistically significant differences from its ancestral form (M), and lost some morphological differences from an allied species *Dysaphis chaerophyllina* Shaposhnikov (C) living on *Chaerophyllum maculatum*. Thus in the fifth generation the differentia between N and M was negligible for two characters: (1) the length of the siphunculi (0.7), and (2) the ratio of the apical rostral segment to the 2nd joint of the hind tarsus (1.3). In the 19th-20th generations the differentia in these characters reached 12.8 and 11.8 respectively. At the same time the differentia between N and C for these characters fell to 0.8 and 2.5. The character of sclerotization (pigmentation) in N is the same as in M.

A long series of experiments on the reciprocal crossing of M, N and C has shown that in spite of the absence of selectivity in mating, the combinations $M \times C$, $C \times M$, $M \times N$ and $N \times M$ (female parent given first) did not lay viable eggs, i.e. practically did not cross.

The combinations $N \times C$ and $C \times N$ gave viable eggs. The fecundity of $N \times C$ was 1·5-4 times higher than that of $M \times M$, $C \times C$, or $N \times N$ (heterosis). On the other hand, in $C \times N$ the fecundity was 5-12 times lower than that in $N \times C$.

According to the traditional concept of a species based on reproductive isolation *majkopica* and *chaerophyllina* should probably be regarded as two good species.

What is this new form? The process of divergence between the new form and its ancestral form *majkopica* resulted in the appearance of a morphological and ecological discontinuity and reproductive isolation. According to the concept mentioned above a specific level of differentiation has been reached. At the same time the new form became more closely, though not completely, related to *chaerophyllina* in its ecology and morphology, and acquired a capability of giving fertile offspring when crossed with it.

Hence the new form should be preliminarily regarded as the repetitive appearance of an already existing species (*chaerophyllina*), but in the shape of a new biotype or a new race. However, since such a form has not been recorded in nature, and has no range of its own, it should be regarded as only a potentiality.

In such cases spatial isolation is not necessary, which indicates the reality of sympatric speciation.

This work should be regarded only as the first steps in this programme. Genetic and particularly cytological investigations are necessary in the future.

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MATHEMATICAL METHODS IN TAXONOMY

CURRENT PROGRESS IN NUMERICAL TAXONOMY

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Many fundamental concepts of systematics such as phylogeny, homology, the biological species and binominal nomenclature have recently been subjected to searching criticism. Ideas and techniques in systematics are in a state of flux and are likely to change considerably in the near future. The new approaches stress operationalism in the establishment of a classification.

Numerical taxonomy has shifted emphasis from genetic to phenetic relationships among organisms. The justification for this procedure is found in modern ideas about the nature of genotype and phenotype as well as in the appropriateness of the study of the phenotype in relation to evolutionary factors. Thus genetic species criteria, while of great importance, are not by themselves sufficient to evaluate the evolutionary potential of a population. Phenetic criteria also permit the consideration of evolutionary change in relation to configuration of ecological niches in their modern interpretation.

The various coefficients of similarity and clustering techniques are being compared and experience with them is accumulating in a variety of groups. New improved statistics of this nature are likely to be forthcoming.

The choice of characters is intimately involved with the nonspecificity hypothesis proposed by Sokal and Sneath (3). Evidence accumulated so far shows that the hypothesis is only partially true, both as regards life history stages as well as congruence between body regions (1 and 2). The magnitude of congruence depends partly on the coefficient of similarity employed. More will be known about the problem of congruence when studies currently underway on larger computers consider the correlations among characters. At least at low taxonomic levels, little congruence is found in different life history stages (4). Studies of correlations of characters will also permit reducing the number of characters employed in a numerical taxonomic study to those representing independent variational trends, thus reintroducing weighting of characters, albeit on an objective basis.

Recent studies have investigated the nature of phylogenetic reasoning and attempted to ascertain the possibility for putting the process on a operational basis. The Kansas group under the direction of Prof. J. H. Camin has used evolutionary lines of imaginary animals possessing a number of morphological characters which were permitted to evolve according to rules unknown to the members of the teams investigating them. Attempts at establishing orthodox phenetic classifications, numerical taxonomic classifications and phylogenetic classifications were made by several teams of investigators. Through discussion and introspection rules of phylogenetic reasoning are being deduced. Independent studies by numerical taxonomy of these groups agree well with taxonomies arrived at by orthodox procedures, but do not represent cladistic phylogenetic relations. It is likely that certain rules for phylogenetic reasoning will emerge from the undertaking.

The advent of numerical taxonomy is also inducing suggestions for changes in biological nomenclature. Such changes should be made both from the point of view of more efficient data handling, i.e. information storage and retrieval, as well as to remove from the present day system of nature certain artificial constraint placed upon it by the binominal system. Most suggestions for revision to date have featured a uninominal system.

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CHARACTER CORRELATIONS IN NUMERICAL TAXONOMY

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The purpose of the present study was to investigate the effects of using a set of highly intercorrelated characters on the results of some of the methods presently used in numerical taxonomic studies.

Forty-five species of North American mosquitoes representing 8 genera and 14 subgenera were studied. The 74 external morphological characters used were taken from the pupal stage and consisted of a set of characters which were expected to be highly intercorrelated. The characters used were: the number of branches of the cephalothoracic setae, the number of branches of most of the dorsal abdominal setae, the lengths of a few of the setae (mostly from abdominal segment I), and various ratios for the paddle and for the respiratory trumpet. The data were taken, with minor corrections, from Barr (1), Darsie (2 and 3), and Price (4).

The data matrix (74 characters by 45 species) was standardized by rows so that each character would have a mean of zero and a standard deviation of unity. Correlation coefficients and distance coefficients (6) were computed for each pair of species. These matrices were analyzed by the unweighted pair group method of cluster analysis using arithmetic averages, UPGMA, (5) to form dendrograms.

Inspection of these dendrograms revealed good agreement with the current classification. However, a few species (*Culiseta melanura, Aedes aegypti, A. triseriatus, A. taeniorhynchus, Anopheles barberi*, and *A. crucians*), especially in the dendrogram based on distance coefficients, were indicated to be much more isolated from their "proper" clusters than one would expect on the basis of the current classification. All of these species, except *A. barberi*, were closest to some members of their own genus but not sufficiently close for the UPGMA to place them into their "proper" groups.

In order to understand more fully the significance of such a relationship, the following additional analyses were performed. Correlation coefficients were computed between all pairs of characters. Centroid factors were extracted from this matrix of correlation coefficients using Thurstone's complete centroid method of multiple factor analysis (with the diagonal elements, h^2, equal to unity initially and the residual h^2 estimated by subtraction). The species were then projected on to the normalized centroid axes. The projections may be interpreted as measurements of each of the species on a set of new characters or components, which are linear combinations of the original characters. They are computed in such a way as to make possible the efficient description of the multidimensional variation among the species in terms of as few dimensions as possible. The variances of the first 13 components were: 26·7, 10·6, 6·0, 5·4, 2·9, 2·2, 2·3, 2·2, 1·7, 1·5, 1·3, 1·3, and 1·2, respectively, indicating that the overall multidimensional variation among the species may be visualized in terms of a hyper-ellipsoid which is particularly elongated in the direction of the first centroid axes, but also in the directions of the second, third, and fourth.

Since the first three factors accounted for an appreciable amount, 58·1 per cent, of the total variation in the study, it was deemed worthwhile to make a 3-dimensional scatter diagram of the species plotted with respect to the first three centroid axes. This proved to be a very useful device for studying the relationships among the species free from the assumptions on which the UPGMA is based, although it contains distortions of its own due to the fact that many centroid axes have been ignored.

The genera were found to form distinct and elongated ellipsoidal clusters, the elongation implying a high degree of correlation among the characters *within* the genera. The character correlation matrices were then computed for the genera *Aedes* and *Anopheles* and for the remaining species separately. A centroid factor analysis were repeated on each of these matrices in order to observe the maximum amount of variation within the genera in 3 dimensions (little additional information was gained by doing this in this particular study since the largest variation within the genera happened to be oriented in a direction similar to that found in the study as a whole). The isolated species listed above (except *A. taeniorhynchus*) were found to lie at the extreme *ends* of their clusters.

Since the UPGMA and related methods cluster with respect to distances between OTU's and, therefore, are biased towards forming hyper-spheroidal clusters, the above results suggest that the methods should be generalized to allow for hyper-ellipsoidal clusters. This can be done by using the amount of variation among the species (as measured by the hyper-volume the cluster occupies) as an index of the level of homogeneity within a cluster rather than by using the average distance between species as is done by the UPGMA.

If the clusters were spheroidal, then the two methods would be equivalent, but if the clusters were elongated, as in the present study, species at the ends of clusters could be added to a cluster in easily or those at the sides of the clusters. This method is being programmed at present.

Alternative procedures involving various transformations of the characters in order to make the clusters as spheroidal as possible were also investigated.

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NUMERICAL TAXONOMY: A CRITIQUE OF THE EFFORTS TO DATE

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1. Numerical taxonomy is inadequate to deal with systematic situations involving adaptive convergence, since these situations may commonly involve too large a proportion of the taxonomic traits available.

2. Examples are cited of likely convergences among animal taxa that would probably be interpreted wrongly by numerical taxonomy, as they often have been by conventional taxonomy.

3. Of these taxa, the rhipiphorid and stylopoid beetles are dealt with in detail, and their non-cognate relationship is demonstrated mainly by their difference in a "minor character," segmentation of the hind tarsus.

4. Weighting of such characters is covered by a proposed *rule of evolutionary reduction*, considered to be implicit in many phylogenetic arguments. This rule is stated formally for the case of meristic characters. *For macroscopic meristic characters in general, a phylogenetic change in number much more frequently results in a decrease than in an increase.*

5. Phylogenetic studies ought to benefit from the conscious application of the reduction rule yardstick and from extension of the morphocline concept of Maslin.

ARACHNIDA, COLLEMBOLA AND HEMIMETABOLA

THE TAXONOMIC STATUS OF SOME MEMBERS OF THE *ONYCHIURUS ARMATUS* SPECIES GROUP (COLLEMBOLA)

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The division of the *Onychiurus armatus* species group by Gisin (2) has been criticised by Stach (4) and Bodvarsson (1). In the present paper Gisin's criteria have been assessed experimentally in four species of the group, namely *Onychiurus procampatus* Gisin 1956, *Onychiurus tricampatus* Gisin 1956, *Onychiurus latus* Gisin 1956 and *Onychiurus fimatus* Gisin 1952, and found to be valid.

In twelve areas examined *O. procampatus* and *O. tricampatus* were found to be present in the same samples; however, in only one area were males of *O. procampatus* found, and the adult males were found to be smaller than the largest adult females. A mean head capsule length of 264 microns was recorded in males as compared with 343 microns in the largest females; a second group of adult females with a head capsule length equivalent to that of the males was also found in the same sampling area. Of the two types of females found, the large variety appeared to be parthenogenetic; it always laid large eggs (230 microns in diameter on laying) which always gave rise to large females, whilst small females laid small eggs (170 microns in diameter on laying) which gave rise to small males and females. However, large females would not lay eggs in isolation, and the presence of small male *O. procampatus* or male *O. tricampatus* was found to be necessary for laying to take place. It seems possible that this is a case similar to that occurring in beetles of the genus *Ptinus* where males of several species can bring about "fertilisation" of female *Ptinus latro* Fab. 1775 (3). Apparently entry of the sperm into the egg of *P. latro* stimulates development mechanically and there is no fusion of the nuclei or exchange of genetic material.

Two types of female (large and small) have also been recorded in *Onychiurus fimatus* and *Onychiurus quadriocellatus* Gisin 1947.

Only sexually reproducing forms of *O. tricampatus* were found and these were equivalent in head capsule length in the adult instars to the small sexually reproducing *O. procampatus*. The fact that *O. tricampatus* was present in the same samples as *O. procampatus* and no intermediates were found between sexually reproducing forms of these two species suggests that they are good species.

During the course of culturing the four species of *Onychiurus* differences in the breeding biology were found. Significant differences occurred between egg-batch sizes of *O. procampatus* (4.6), *O. tricampatus* (9.7) and *O. latus* (15.1). In *O. latus* maximum head capsule length was reached in the 7th instar, in the other three species in the 6th. instar. In the field egg laying took place in spring in *O. latus* and throughout the summer in *O. procampatus* and *O. tricampatus*. In the last two species there was a significant difference in their vertical distribution, *O. tricampatus* occurring deeper in the soil.

Since the chaetotaxy and pseudocellar formula are identical in the same instars of sexual and parthenogenetically reproducing forms, and since there is a size difference in these forms (parthenogenetic 1st instars are equivalent in head capsule length to 3rd instars of sexually reproducing forms), this has probably given rise to the claim that individuals of similar size possess different pseudocellar formulae and chaetotaxy. In the species studied in the present work the criteria of Gisin (1952) for the division of the *Onychiurus armatus* species group are valid, since they are consistent from generation to generation and true intermediates do not exist; biological differences also occur in these four species.

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THE CLASSIFICATION OF EPHEMEROPTERA IN RELATION TO THE EVOLUTIONARY GRADE OF NYMPHAL AND ADULT STAGES

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Ephemeroptera imagos have been subject to natural selection associated primarily with reproduction. Nymphal features have evolved for life in a diversity of aquatic habitats. Most of the structures evolve semi-independently in the two stages. Inferences concerning phylogeny which are drawn from the adults thus may be tested by comparison with inferences drawn from the nymphs. Groups that are separated from their nearest relatives by extremely wide gaps in one stage may show only slight differentiation in the other stage; no rule may be formulated as to which stage evolves more rapidly.

Any classification that is based on one life history stage is at times inconvenient for considering the other stage because the size and position of the character gaps employed in hierarchic categorization are different in the adult and nymphal stages. Following are some of the outstanding examples from the Ephemeroptera.

In the Tricorythidae, such unique and specialized nymphs as *Diceromyzon* and *Machadorythus* might well be placed as the sole members of monotypic families, except that the known adult structures appear to be rather typical of the Tricorythidae. A more striking case is seen in the Neoephemeridae and Caenidae. These two families are almost indistinguishable in the nymphal stage, being virtually impossible to separate except on size and the presence or absence of the developing hind wings. But the families are so completely different in the adults that as yet no characters have been found in the exoskeleton that will serve to characterize the group. Thus, although the nymphal evidence suggests that there is no justification for two families, the immense character gap between the adults of the two groups favors the separation into two families.

In the family Siphlonuridae (including Isonychiidae) the nymphs have evolved more rapidly than have the adults. Such subfamilies as Ameletopsinae, Oniscigastrinae and Coloburiscinae each have many unique nymphal characters and would seemingly be more convenient to regard as distinct families, except that the adult characters appear to be few even for their segregation as subfamilies. Another type of problem arises in the Siphlonuridae because it appears highly probable that the nymphal traits of most other families of Heptagenioidea can be traced into the Siphlonuridae. Thus some of the nymphs now placed in the Siphlonuridae would be best considered as primitive members of other families except for the fact that the adults largely retain Siphlonurid characters.

The phylogenetic interrelationships of most genera of Ephemeroptera are now reaching fairly reliable levels of probability. This has been possible because of the wide range of characters studied by various investigators, the extensive geographic areas represented, and the fact that about 80% of the named genera are known in the nymphal stage by one or more described species. The probable phylogenetic sequence is best represented by means of a phylogenetic tree diagram, but the classification must consider not only phylogeny but historical stability, utility, and the conceptual value of the generalization expressed by the hierarchic arrangement as it applies to both nymphal and adult stages.

L'EXAMINATION DE LA VALENCE DES FORMES DU GENRE *PSORODONOTUS* FICH (ORTHOPTERA) DE PENINSULE DES BALKANS

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D'après les derniers travaux de Ramme (3) et de Karabag (1, 2) le genre *Psorodonotus* comprend 13 espèces balkanoanatoliennes, dont 6 habitent le territoire de Caucase, 3 sur le Péninsule des Balkans et 4 dans l'Asie Mineur.

Le nombre insuffisant des exemplaires, surtout de séries des préparations d'organe copulateur fûrent la cause des traitements erronés des formes balkaniques du genre *Psorodonotus.*

Nos examinations executées sur le terrain et les matériaux obtenus des plusieurs musées ont démontré qu'il n'existe sur le Péninsule des Balkans que deux espèces endemiques de *Psorodonotus. P. fieberi* F r i v. habite la Serbie et la Bulgarie et *P. illyricus* E b n e r l'Istrie, le littorale croate, la Bosnie et l'Herzégovine, la Monténégro, la Macedoine et l'Albanie. Sur le mont Ivan et à Ulog on trouve une forme nouvellement décrite—*f. grandis* Miksić. Les exemplaires de Monténégro apparaissent comme les formes transitoires entre *P. illyricus* f. t. et ssp. *macedonicus* Rme. Celle-ci habite la Macedoine et l'Albanie.

En comparant les formes balkaniques aux autres espèces du genre *Psorodonotus* d'après quelques caractères taxonomiques on aperçoit une ressemblance qui indique d'une certaine manière la voie évolutive de ce genre. D'après la structure de l'organe copulateur *P. fieberi* se distingue des autres espèces et représente un ancien type. La voie évolutive mène du type primaire à l'étrécissement du point du titillateur, à la reduction du nombre de dents, à l' accourcissement des cerques et à l'allongement de leur dent laterale. Cette évolution représente probablement le reflet de la migration d'espèce.

Vers l'occident *P. fieberi* a perdu au cours de son expansion plusieurs dents de titillateur et les cerques se sont raccourcis. Cette voie a mené d'abord vers le sud (*P. illyricus* ssp. *macedonicus*) et puis à travers de Monténégro vers nord-ouest.

A l'orient *P. fieberi* passa à travers la Roumelie et atteigna l'Asie Mineur. Chez les espèces d'Asie Mineur, qui s'approchent à *P. fieberi* on apercoit aussi la disparition de dents du titillateur (*P. anatolicus*) tandis que l'élargissement du point du titillateur en est encore plus au moins gardé (*P. rugulosus* et *P. ebneri*).

Sur le territoire de Caucase et de Transcaucasie arriva la même chose qu'à l'ouest. Les titillateurs n'ont pas le point élargi, en exceptant *P. causasicus,* qui représente ici probablement la forme la plus ancienne et dont la valence systématique n'est pas encore confirmé. Les cerques deviennent plus courts. De cette manière la structure de l'organe copulateur des espèces caucasiennes rappelle beaucoup à celle des espèces balkaniques.

Chez les femelles ont peut suivre dans une certaine mésure le develloppement de l' oviscapte. Ainsi on aperçoit que chez les espèces dont les mâles ont un titillateur plus au moins élargi l'oviscapte est plus au moins court. Cependant l'évolution de cet organe correspond à l'évolution des caractères morphologiques extèrieurs et les organes copulateurs des mâles étant des organes intérieurs, sont naturellement les meilleurs indicateurs au sens évolutive.

L'élaboration des complets matériaux documentaires sur ce thème sera publié à part, sous le même titre dans GZM à Sarajevo en 1964-65 année.

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TOWARDS A NATURAL CLASSIFICATION OF THE DERMAPTERA

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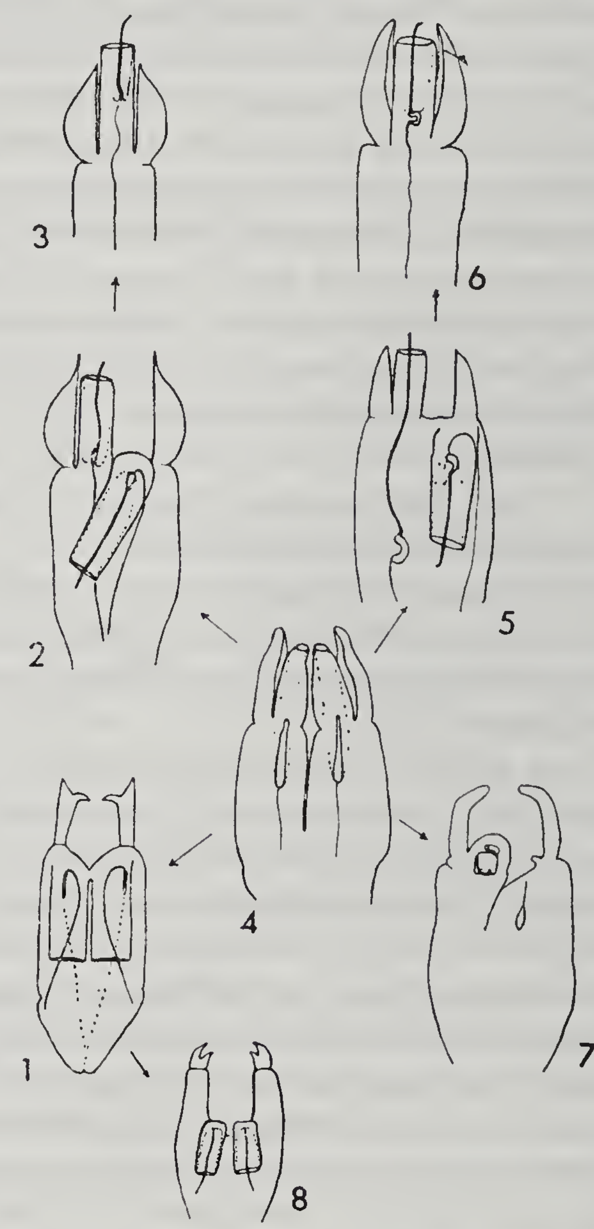
The Dermaptera are very uniform, and their systematics present special problems. The use of such vestigial characters as the gonapophyses of the females or the opisthomeres of both sexes has resulted in confusion and disagreement. The current classification based upon the work of Verhoeff (3), Zacher (4) and Burr (1) on the external male genitalia may be summarised as follows:

The Pygidicranidae have two functional penis lobes, which are normally flexed forwards when not in use (fig. 1). The Labiduridae have two penis lobes one of which is directed backwards and the other, which is non-functional is permanently directed forwards (figs. 2 and 5), while the Labiidae, Chelisochidae and Forficulidae are grouped into a single super-family on account of their single median penis lobe (figs. 3 and 6). The following facts imply that the classification is not a natural one.



Figs. 1-8. Male genitalia of Dermaptera.

1. In the Thysanura and Ephemeroptera, the penis lobes of the males are directed backwards and the Pygidicranidae are therefore, unlikely to be quite as primitive as has previously been supposed.

2. *Parisopsalis spryii* Burr (fig. 4) (Parisolabinae) has two penis lobes which are directed backwards and the form of the external male genitalia of this earwig is, therefore, more primitive than that of other earwigs and suggests that the form of the external male genitalia in the Labiduridae is more primitive than that of the Pygidicranidae (fig. 4).

3. The Pygidicranidae are unrepresented in New Zealand and only two of the eight sub-families occur east of Wallace's Line, whereas the unspecialised Labidurid subfamilies of

the Parisolabinae and Brachylabinae have a wider geographical distribution from New Zealand to South America, while the primitive Nesogastrinae (Labiidae) also occur in New Zealand.

These three sets of facts suggest that the male genitalia of the Labiduridae are probably more primitive than are those of the Pygidicranidae.

4. The Labiidae, on the one hand and the Forficulidae and Chelisochidae on the other, can be distinguished by the following characters.

(*a*) The virga of the Labiidae never has a basal reniform vesicle; a feature which is always present in the Chelisochidae and Forficulidae.

(*b*) In the Labiidae, the second tarsal segment is simple and not extended ventrally under the third or distal segment, as it is in the other two families.

These differences can also be used to separate the subfamilies of the Labiduridae into two groups as follows. The Parisolabinae, Brachylabinae, Platylabinae and Carcinophorinae resemble the Labiidae, while the Allostethinae, Labidurinae and Apachyinae resemble the Forficulidae and Chelisochidae (cf. figs. 2-6).

5. The form of the external male genitalia of the Karschiellinae is so highly specialised that it bears little similarity to that of any other group of earwigs (fig. 7).

These facts suggest that the various subfamilies should be regrouped and that a more natural classification of the Dermaptera might be as follows.

Superfamily Labioidea
1. Carcinophoridae; Subfamilies:—Parisolabinae, Brachylabinae, Carcinophorinae and Platylabinae
2. Labiidae
3. Arixenidae

Superfamily Forficuloidea
1. Labiduridae; Subfamilies:—Labidurinae, Allostethinae, and Apachyinae
2. Chelisochidae
3. Forficulidae

Superfamily Pygidicranoidea
1. Diplatyidae; Subfamilies:—Cylindrogastrinae, Diplatyinae
2. Pygidicranidae; Subfamilies:—Pygidicranidae, Anataelinae, Echinosomatinae, Blandicinae, Esphalmeninae and Pyragrinae

Superfamily Karschielloidea
Karschiellidae Sub-family:—Karschiellinae

Previous studies on the Hemimerina have shown that they are best regarded as a separate order of insects (2).

The Arixenidae show trends similar to those of the rest of the Dermaptera and it seems best to give them family status within the Labioidea.

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NEUE ASPEKTE IN DER TERMINOLOGIE DES APHIDOIDEA-GENERATIONS- UND WIRTSWECHSELS[1]

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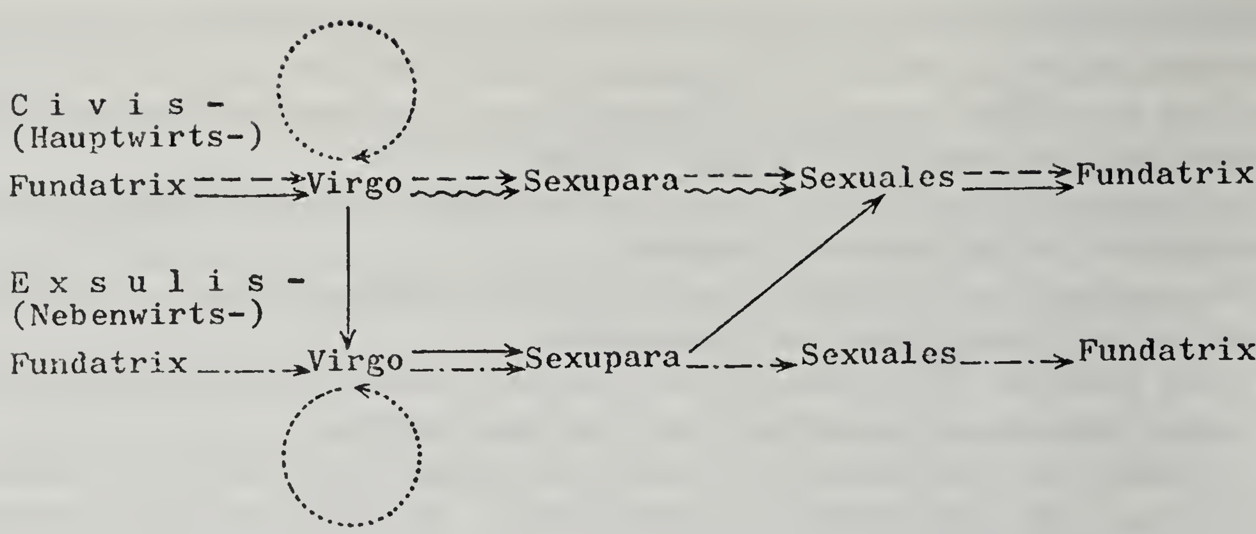
Im Gegensatz zu den ursprünglichsten Aphidoidea, die nach Mordwilko (1928) nur aus geflügelten ♂♂ und ♀♀ bestanden, haben wir heute infolge des Aufkommens eines Generations— und Wirtswechsels eine gewaltige Morphenfülle innerhalb der Blattlauszyklen (welche ein- oder zweijährig sein können) vor uns. Eine erste Benennung der Morphen wurde zwischen 1880 und 1910 durchgeführt, doch müssen wir uns fragen, inwieweit wir heute noch mit diesen

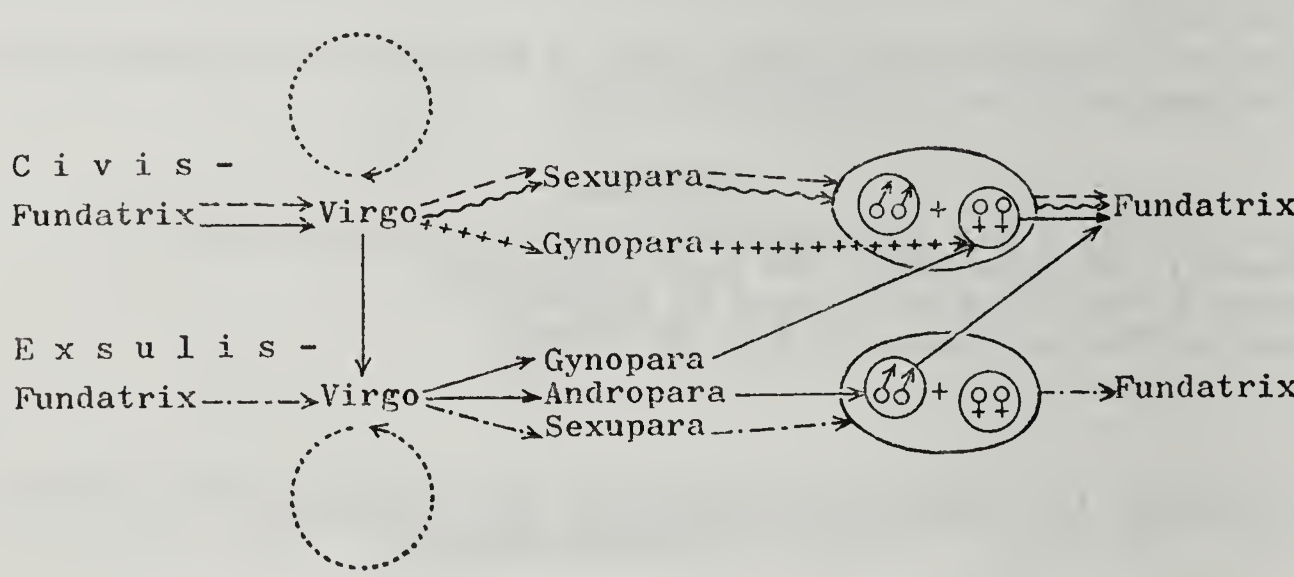
[1. Eine ausführliche Arbeit Über die Aphidoïdea-Generationswechsel-Biologie wird demnächst erscheinen.]



——— = obligatorischer Wirtswechsel (obligatorische Heterözie)
– – – – = Eu- und Paramonözie am Hauptwirt
—·—·— = Paramonözie am Nebenwirt
——— + ~~~~ = fakultativer Wirtswechsel (fakultative Heterözie)
.... = Anholozyklie oder Parazyklie

Abb. 1: Schema einer einheitlichen Terminologie für die Morphenfolge der Aphidoidea

klassischen Termini auskommen, beziehungsweise ob deren Anwendungsbereiche noch zutreffen. Vor allem die Ergebnisse phylogenetischer Studien sind es, die heute das alte klassische Bild von Haupt- oder Primär- und von Neben-, Zwischen- oder Sekundärwirt ins Wanken gebracht haben. Neben wirtswechselnden (heterözischen) und primär nichtwirtswechselnden (eumonözischen) (5) Arten kennen wir nämlich heute auch solche monözische Arten (Paramonözier), die sekundär aus wirtswechselnden Vorfahren entstanden sind, sei es am Haupt-, sei es am Nebenwirt; und den Paramonöziern am Nebenwirt ist es dabei gelungen —im Gegensatz zu den Anholozykliern, das heißt denjenigen Arten, die die bisexuelle Fortpflanzung völlig aufgegeben haben—die Morphe der Fundatrix und die Generation der Sexuales mit auf den Nebenwirt herüberzuziehen (*Neanoecia*, *Paranoecia* unter den Thelaxidae, manche Aphididae). Die alte Blochmann-sche, 1889 aufgestellte Hauptwirtsdefinition, welche besagt, daß die "Geschlechtsgeneration", d.h. die Sexualis- oder besser bisexuelle Generation, (nur) am Hauptwirt (einer bestimmten Blattlausgruppe) lebt, ist somit hinfällig geworden.



——— = obligatorische Heterözie
– – – – = Eu- und Paramonözie am Hauptwirt
—·—·— = Paramonözie am Nebenwirt
——— + ~~~~ = fakultative Heterözie
——— + ++++++ = partielle Spanandrie
.... = Anholozyklie oder Parazyklie

Abb. 2: Die Morphenfolge bei den Aphididae

Vor allem auf Grund dieser Tatsache möchte ich im folgenden eine neue Art der Terminisierung der Blattlaus-Zyklen vorschlagen, die gleichzeitig den Vorteil hat, die Verhältnisse aller Arten, seien es eu-oder paramonözische oder anholozyklische am Hauptwirt, paramonözische oder anholozyklische am Nebenwirt oder obligatorisch beziehungsweise fakultativ heterözische, einzuschließen (und die mit einer kleinen Änderung auch für Subheterözier gilt). Dies wird durch die Gebung von Doppelnamen erreicht. Es werden die Termini Fundatrix, Virgo, Sexupara und Sexuales in je ein alternatives Begriffspaar aufgelöst. Die Hauptwirtstiere stelle ich dabei unter den Oberbegriff der "*Civis*", die Nebenwirtstiere unter den Oberbegriff der "*Exsulis*", wobei sich der letztere Terminus von seiner bisherigen Anwendung für eine rein virginogene und virginopare Form zu einem Oberbegriff für alle Morphen am Nebenwirt, bei Paramonöziern also auch für Fundatrix und Sexuales, verschiebt. Abbildung 1 zeigt in kurzer Übersicht, wie man die verschiedensten Verhältnisse unter einen Hut bringen kann. Kurz möchte ich darauf hinweisen, daß in meiner neuen Terminologie die Börnerschen Begriffe Fundatrigenia und Virginogenia (e) verschwunden und dadurch die bisher vorhandenen begrifflichen Schwierigkeiten (zum Beispiel entstehen ja alle Morphen außer der Fundatrix parthenogenetisch, "virginogen") beseitigt worden sind.

Für diejenigen Aphidoidea, deren wirtswechselnde Arten eine Trennung der Sexupara-Morphe in Gyno- und Andropara besitzen, also vor allem die Aphididae, kompliziert sich das Schema etwas. Dies zeigt Abbildung 2. (Die monözischen Arten der Aphididae sind hierauf als sexupar angegeben, wie es die Regel ist).

Bei Subheterözie, der Vorstufe des Wirtswechsels, das heißt bei Platzwechsel an der gleichen Wirtspflanze, wie er bei einigen Lachnidae, Aphididae und bei *Viteus vitifolii* (Fitch 1855) Shim. 1867 vorkommt, wird der Begriff der Exsulis in Proëxsulis abgeschwächt. Die Rückkehr vom Ort der Proëxsules zu dem der Cives wird entweder von der Sexupara (Reblaus) oder aber erst von den Sexuales durchgeführt (6).

So wie die Subheterözie ein Sonderfall als Vorstufe des Wirtswechsels ist, sind Parazyklie und Spanandrie Sonderfälle als Übergangsstufen zwischen Holozyklie und Anholozyklie. Parazyklie und Anholozyklie sind in Abbildung 1 und 2 in Form kleiner Kreise dargestellt, wobei der Unterschied zwischen Parazyklie und Anholozyklie darin besteht, daß bei letzterer die Kreise in sich selbst geschlossen sind, während bei ersterer noch ein Anschluß an die übrigen Morphen möglich ist. Bei Spanandrie—wie sie bei den Pineinae unter den Adelgidae auftritt (3)—bleiben vom Gesamtschema nur folgende Morphen übrig: Exsulis-Virgo, Exsulis-Gynopara und Civis-Sexualis-Weibchen. Die Gynopara fliegt zwar noch auf einen Hauptwirt über, dort vollendet sich der Zyklus infolge des Fehlens von Männchen aber nicht mehr.

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SOME ADVANCES IN THE TAXONOMY OF THE COCCOIDEA (HOMOPTERA)

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In basing the taxonomy of the Coccoidea mainly on the morphology of the degenerate adult females only a fraction of the potential information is used. Not surprisingly, the affinities of many forms are still obscure. Today taxonomically important results are also obtained from the study of aspects such as the morphology of sperm bundles, host/symbiont relationships, cytological mechanisms and adult male morphology.

In the Pseudococcidae Doutt (1952) found that categories of species based on sperm bundle similarities closely conformed with the generic classification of Ferris (1950). Nur (1962) found that sperm bundles differed in other groups as well and that those of *Puto* and *Rhizoecus* differed substantially from the other *Pseudococcidae.*

Walczuch (1932) and Buchner (1953, 1955) showed that there are many different coccid symbionts, which are in a variety of ways associated with their hosts and in equally diverse ways transferred to the oocytes. They found conditions within higher taxa often remarkably constant. However, conditions in various subfamilies of the Margarodidae vary considerably and those in the pseudococcid genera *Puto* and *Macrocerococcus* differ substantially from all other coccids.

A very wide range in diverse and unique cytological mechanisms have been evolved in various groups (Hughes-Schrader, 1948; Brown and McKenzie, 1962). Some Margarodidae retain the ancestral XX-XO sex determining mechanism and share this with *Puto* and probably (Buchner, 1955) *Macrocerococcus* amongst the lecanioids. In the asterolecaniid *Mycetococcus* Brown and McKenzie discovered the *Comstockiella* system of chromosome behaviour (which is otherwise only found in the diaspidoids) and suggested that the Diaspididae originated from the Asterolecaniidae.

The morphology of male Coccoidea recently received considerable attention. Theron (1958) suggested homologies for the various structures. Subsequently numbers of species were studied in the Pseudococcidae (Beardsley, 1960, 1962; Giliomee, 1961), Coccidae (Giliomee, unpublished) and Diaspididae (Ghauri, 1962). These studies proved that male characters were useful and valid at all taxonomic levels. *Puto* and *Macrocerococcus* differ sharply from all other Pseudococcidae and the three Margarodidae from each other.

Conclusions: (*i*) The division of the Coccoidea into three sections (Balachowsky, 1948) is substantiated by detailed studies of the chromosome mechanisms and the male morphology. The margarodoids are the most primitive and the diaspidoids the most specialized Coccoidea, (*ii*) Certain genera share important features with two sections: *Steingelia, Phenacoleachia, Puto* and *Macrocerococcus* with the margarodoids and lecanioids, and *Mycetococcus* with the lecanioids and diaspidoids. These genera may indicate evolutionary pathways. (*iii*) If the diversity in the various aspects of the Margarodidae is valid at the same taxonomic levels as in the other Coccoidea, subfamilies or groups of subfamilies within the Margarodidae deserve family rank. (*iv*) *Puto*, together with *Macrocerococcus,* should be separated from the other Pseudococcidae and given a subfamily or even family rank.

HOLOMETABOLA

EVOLUTION AND GENETICS OF HAWAIIAN DROSOPHILIDAE

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The family Drosophilidae is the largest known group of animals in Hawaii and represents one of the most unusual developments of this family in any area of the entire world. We have here a remarkable example of rapid explosive evolution which is almost unparalleled in the animal kingdom and the Hawaiian Islands should be the most ideal area in the world for studying evolution and speciation in the drosophilids.

Volume 12 of "The Insects of Hawaii" series which is now in press deals entirely with the family Drosophilidae and treats 400 species of which 243 belong in the genus *Drosophila* and 114 in the genus *Scaptomyza*. This is the greatest known concentration of these genera of any known area of the world. Since this volume has gone to press at least 50 additional new species have been collected and it is now estimated that the total number of species may be 550-600.

The evolution and genetics study is being conducted as a cooperative project between the University of Hawaii and the University of Texas Genetics Foundation and involves detailed field and laboratory research carried on by a team of visiting scientists.

The first objective has been to learn how to establish native species in artificial media. Considerable success has been achieved and approximately 36 species have now been reared through the F_3 generation and some are now being used for genetic studies. The successes have resulted from the knowledge gained about the breeding habits and food requirements and entirely new rearing technics and food media have been devised. To date it appears obvious that the Hawaiian species feed largely upon various fungi, and probably assorted organisms in leaf mold and they require a diet much higher in proteins than has previously been used for raising *Drosophila*. The development of a high protein diet by Drs. M. Wheeler and F. Clayton has been one of the major breakthroughs in this study.

Extensive collections are being made throughout the islands to gain as complete a knowledge as possible of the taxonomy and distribution of the species and studies are being conducted which should provide valuable data concerning phylogenetic relationships and the evolutionary sequences of the species. To date we have little knowledge concerning the phylogenetic significance of the peculiar morphological characters exhibited by the Hawaiian species and it is obvious that such knowledge will have to be gained by combining information gathered from studies of external and internal morphological characters, of the immature stages, the breeding habits, mating behavior, cross-breeding experiments, and by biochemical and cytological studies. In this regard the most useful tool to date has been the comparative studies of internal morphology being conducted by Dr. Lynn Throckmorton.

From the evidence now at hand it appears probable that the entire endemic fauna of Drosophilidae could have originated from one ancestral species.

This is planned as a long-range project which should result in much valuable data concerning modes and rates of evolution in insular areas. Attempts will also be made to determine the probable origin of Hawaiian species and the possible paths of dispersal of Drosophilidae throughout the Pacific region.

THE AFRICAN SCOLIIDS AND THEIR AFFINITIES

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The Tribe Trielini of the subfamily of the Campsomerinae consists of three genera: *Guigliana* Betr., *Crioscolia* Bradley and *Trielis* Sauss.

Guigliana is African, not only Ethiopian; one of the subgenera occurs in North Africa and Palestine. Subgenus *Guigliana* lives from the southern border of the Sahara through East Africa to Mozambique. It prefers dry areas. Other subgenera occur in the Cape Province and on Madagascar.

The genus *Crioscolia* has a very discontinuous distribution: the western dry part of the U.S.A., Algeria, Turkestan, Mongolia and around Lake Nyasa. It also prefers dry regions.

The genus *Trielis* consists of three subgenera. The subgenus *Trielis* occurs over a large part of the U.S.A. and Southern Europe eastwards to Russia. It is not restricted to truly arid areas, but it does not live in wet areas. The second subgenus *Heterelis* is distributed through the whole southern Palaearctic eastwards to Pakistan and Turkestan, it also occurs in North Africa; a separate species can be met in a rather small area in the Cape Province. A third subgenus has been found only in South and South West Africa.

The Trielini are an old group with a relict distribution. This taxon is absent in the wet parts of Africa. The species occur mostly in dry areas, but some in countries with a mediocre rainfall. These facts point to the possibility that the climate of Africa was dry in former geological times.

All African subgenera of the genus *Campsomeris* are restricted to the Ethiopian region except *Micromeris* and *Campsomeriella*. Both of these are present in the wet as well as in the dry parts of Africa. They invaded in some waves the Indoaustralian Region. *Micromeris* reached the Moluccas, *Campsomeriella* New Guinea and the Solomon Islands. They form the only western elements in the Scoliid-fauna of the Indoaustralian Region. Many other Indoaustralian taxa are immigrants from Central China. One of the reasons that the other subgenera of *Campsomeris* did not migrate into the Indoaustralian Region can be that their representatives are stenoöecous and not euryöecous as are *Micromeris* and *Campsomeriella*.

A very striking example of Müllerian mimicry occurs in different genera of the Scoliidae, in *Liacos*, *Campsomeris* and *Scolia*, in Africa. All three are black with black vestiture. The wings are only partly black, their hind-parts and ends being hyaline in such a way that it appears that the wings are folded longitudinally when they lie on the back of the insects. They mimic large black vespids. Professor Van der Vecht thinks that they probably mimic *Eumenes emarginatus* (L) (= *E. maxillosa* de Geer), a common large black wasp. The scoliid species that show this mimicry are distributed from Western Africa to Kenya and Mozambique.

CARACTERES SPECIFIQUES MIS EN EVIDENCE CHEZ LES ICHNEUMONIDES PAR DES RECOLTES MASSIVES[1]

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Des captures massives effectuées durant une quinzaine d'années sur le rivage méditerranéen, m'ont permis d'éclaircir la systématique de nombreux groupes d'Ichneumonides et de mettre en évidence des caractères spécifiques nouveaux dans la plupart des genres.

Les caractères de la couleur ne sont ni plus ni moins importants que les particularités structurelles. La couleur, tout comme la structure, appartient à la définition de l'espèce: elle est parfois fort variable, mais elle varie seulement entre des limites fixes.

Par exemple, on parvient à distinguer certains mâles de *Scambus* à la couleur du pédicellus antennaire, tandis que les tibias III présentent chez les *Exochus*, des gammes de coloration tout à fait spécifiques.

Les *Hyposoter* du groupe de *H. caedator* Grav. ne diffèrent-ils pas des autres espèces du genre, par leurs tibias assombris à la base même, et non à une certaine distance de l'articulation?

Enfin, dans les genres *Casinaria*, *Campoplex*, *Sinophorus* (= *Eulimneria*) et *Diadegma* (= *Angitia*), maintes espèces vont de pair, les unes ayant les tibias III blancs au milieu, les autres des tibias rouges ou jaunâtres.

Or, on constate que les espèces en question ne cohabitent pas: tributaires sans doute d'exigences écologiques différentes, elles volent dans des localités distinctes au sein d'une même région faunistique.

L'absence d'intermédiaires entre certaines colorations extrêmes, peut également être considérée comme un indice de spécificité.

Comme ceux de la couleur, les caractères structurels sont fort divers d'un genre à l'autre: chez les Pimplinae *Itoplectis*, certaines espèces sont reconnaissables à la forme du denticule, à peine perceptible sous la griffe antérieure de la ♀, caractère d'autant plus important et spécifique, que les espèces en question ne présentent aucune interattraction sexuelle et ne s'hybrident pas.

Chez les *Ephialtes*, les *Aritranis* (= *Hoplocryptus*), les *Opidnus* (*Microcryptus* auct.) et les *Netelia* (= *Paniscus*), l'extrémité de la tarière présente d'importants caractères spécifiques, notamment le nombre et la disposition des dents de scie visibles sur les stylets.

Très importante chez les *Ichneumoninae*, la longueur des articles antennaires les uns par rapport aux autres, m'a également permis de séparer deux espèces méridionales du genre *Orthocentrus*.

Dans les genres *Epitomus* et *Gelis* par contre, ce caractère varie, mais on peut distinguer certaines espèces à la structure de leur sulcus genalis qui est plus ou moins marqué.

Enfin, les denticules du clypéus diffèrent d'une espèce à l'autre chez les mâles de *Phygadeuon*, tandis que certaines espèces des genres *Trychosis* (= *Goniocryptus*) et *Dusona* (*Campoplex* auct.) sont reconnaissables à leur carène génale plus ou moins développée.

Les captures massives ont également révélé des cas extrêmes de dimorphisme sexuel, le scutellum étant plus convexe, le pétiole plus large à la base, les carènes métathoraciques plus fortes chez les mâles que chez les femelles du genre *Hypsicera* (= *Metacoelus*).

Par ailleurs, chez les mâles d'*Helictes*, l'abdomen est plus brillant que chez les femelles, l'une des raisons justifiant la mise en synonymie d'un grand nombre de prétendues espèces décrites par Förster.

[1. Contribution à l'étude des Hymenoptères No. 48 (voir No. 47 in Mitt. Schweiz ent. Ges., 37: 3, 1964.]

LA SUPERFAMILLE DES CYNIPOÏDES (HYMENOPTERA) DANS LA REPUBLIQUE POPULAIRE ROUMAINE

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Des 11 ou 12 sous-familles que comprennent les Cynipoïdés, en Roumanie on en connaît 7 qui sont: *Ibaliinae*, *Eucoilinae*, *Aspicerinae*, *Anacharitinae*, *Figitinae*, *Charipinae* et *Cynipinae*. Les sous-familles: *Oberthuerellinae*, *Liopterinae*, *Mesocynipinae* et *Pycnostigmatinae* ne se trouvent pas dans la faune de la Roumanie.

Parmi ces sous-familles, la mieux représentée est la sous-famille *Cynipinae* qui comprend, 27 genres avec 118 espèces dont 103 espèces sont gallicoles et 15 espèces commensales. Les genres les plus riches en espèces sont: *Andricus*, *Adleria*, *Neuroterus* et *Cynips*.

En ce qui concerne leurs affinités zoogéographiques, en rapport avec l'expansion des Cynipidés gallicoles en Europe, on constate que 50% des espèces ont des affinités pour l'Europe centrale et méridionale tandis que les espèces caractéristiques de l'Europe centrale et Occidentale ne sont représentées, en Roumanie, que par peu de formes.

Les Cynipoïdés parasites comptent un nombre de 99 espèces comprises en 34 genres. La sous-famille *Ibaliinae* est représentée par un seul genre connu *Ibalia*, avec une espèce. La sous-famille *Eucoilinae* par 17 genres avec 49 espèces. La sous-famille *Aspicerinae* par 3 genres avec 3 espèces. La sous-famille *Anacharitinae* par 2 genres avec 3 espèces. La sous-famille *Figitinae* par 6 genres avec 12 espèces. La sous-famille *Charipinae* par 5 genres avec 31 espèces. Les mieux représentées sont les *Eucoilinés* avec 50% des espèces, puis les *Charipinés* avec presque 30%. En ce qui concerne l'expansion des Cynipoïdés parasites en Roumanie, la répartition est la suivante: dans la région montagneuse 23 espèces de 13 genres; dans le nord du pays 19 espèces de 12 genres; dans le sud du pays 24 espèces de 15 genres; dans la région montagneuse et la plaine du sud du pays 4 espèces de 4 genres; largement répandues dans le pays 9 espèces de 7 genres; en Dobroudja 9 espèces de 7 genres.

Le genre ayant la plus grande expansion en Roumanie est *Charips*, dont les 21 espèces sont répandues dans tout le pays, du Nord au Sud, à la montagne et à la plaine. Puis vient le genre *Kleidotoma* avec 13 espèces, de même sur tout le territoire roumain.

La plupart des genres et des espèces sont répandus dans le sud du pays, puis vient un nombre de genres et d'espèces tout aussi grand dans la région montagneuse. Les espèces et les genres ayant une grande aire en Roumanie sont peu nombreux. Le plus petit nombre d'espèces est dû à celles dont l'aire comprend et la région de montagne et celle de plaine. Il en résulte la dépendance étroite des espèces et du climat; dans notre pays, sur des espaces peu étendus, on trouve des conditions climatiques très variées. Il existe aussi des espèces dont l'aire comprend des régions de climats très différents, montagne et plaine chaude du sud du pays, mais leur nombre est très petit (4 espèces de 4 genres).

FAMILIES AND GENERA OF MECOPTERA

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Supposed generic groups of extant Mecoptera were compared on the basis of 88 selected characters of the head (22), wings (18), thorax and legs (16), male abdomen (22) and female abdomen (10). Fossil forms were excluded, and no attempt was made to reconstruct phylogeny. Degree of relationship was judged from the number of matches (agreement in state or condition of a character), number of mis-matches, and number of characters that could not be compared. Because the Mecoptera are an ancient order, well diversified even in the Permian period, the view is taken that living forms represent survivors of widely divergent lines of evolution. Accordingly, diverse groups are given generic or familial status depending upon their level of correlation rather than assigned to fewer and larger taxa on the basis of a few similarities.

Merope and *Austromerope*, agreeing in 83 of 88 compared characters but neither sharing more than 69 with any other genus, comprise a distinct family (Meropeidae). Similarly, *Nannochorista* and *Choristella*, with 84 characters in common but neither agreeing with any other genus in more than 61, are combined in the family Nannochoristidae.

Chorista and *Taeniochorista* (family Choristidae) have 80 matching characters but do not form as distinct a family as the Meropeidae or Nannochoristidae. Their higher average correlation with all family groups in the order than any other family suggests they may possess more common ancestral characters; and in wing venation, at least, they most nearly resemble the Permian forms.

Notiothauma, sharing only 62 characters with the Choristidae and fewer with other genera and families, and *Boreus*, agreeing with other genera in only 38 to 50 characters of the 88, form distinct families, respectively Notiothaumidae and Boreidae.

Winged genera of Bittacidae have 79 to 87 matching characters (mean 83), but between these as a group and the two flightless genera the average number of matches is only 68, resulting from 14 non-comparable characters but only 6 that are mis-matched.

In the family Panorpidae, as currently recognized, *Panorpa*, *Neopanorpa* and *Leptopanorpa* are closely interrelated, averaging 85 matching characters. *Neopanorpa* and *Leptopanorpa*, with 87 matches, are judged distinct on the basis of characters not included in this comparison.

Panorpodes and *Brachypanorpa* comprise a compact group, with 82 matching characters but averaging only 72 matches with the Panorpidae *s.s.* This suggests greater affinity between these two groups than exists between winged and flightless bittacids. Between the bittacid groups, however, there are only 6 mis-matched characters, while there are 16 between the panorpid groups. Since the Panorpidae *s.s.* are saprophagous and *Brachypanorpa* (and by inference *Panorpodes*) phytophagous, and since there are profound differences between larvae of the two groups, *Brachypanorpa* and *Panorpodes* are placed in a separate family, Panorpodidae.

The remaining genus, *Apteropanorpa*, shows no close relationship to any other genus. It has about equal affinities with Choristidae and Meropeidae (average of 50 matches, 21 mis-matches, 17 non-comparable characters, due largely to absence of wings). In contrast, it has only 45 matches but 25 mis-matches with the Panorpidae *s.s.* Since *Apteropanorpa* appears more isolated from other Mecoptera than either *Boreus* or *Notiothauma*, it is placed in a distinct family, the Apteropanorpidae (new family, including at present only *Apteropanorpa tasmanica* Carpenter, 1941).

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ZWEI JARHUNDERTE SYSTEMATIK DER KÖCHERFLIEGEN (TRICHOPTERA)

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Die Gattung *Phryganea* von Linnaeus umfasste bei ihrer Gründung (1758) 17 Arten. Als nicht hierzu gehörend wurden später vier Arten ausgeschieden, so dass unsere Kenntnis der trichopterologischen Systematik mit 13 Arten anfing. Heute sind mehr als 5000 Arten bekannt, verteilt über 26 Familien. Die Literatur ist so umfangreich, dass ich für die systematische Zusammenstellung im Trichopterorum Catalogus nicht weniger als 15 Bände von 200 bis 250 Seiten brauche.

Die Fortschritte der Trichoptera-Systematik werden chronologisch behandelt, besonders die Verteilung in Familien und die Identifizierung der alten Arten. Es wird angenommen, dass die Zahl der Familien auf 40 oder sogar 50 ansteigen wird. Weltumfassende Monographien von ganzen Familien werden erwähnt und die Geschichte der alten und der jetzt gebräuchlichen Zweiteilung der Ordnung wird behandelt.

Tabelle I

Familien	*Genera*		*Synonyme*	*Spezies (inkl. fossile)*		*Synonyme*		*Fossile Spezies*	
	1938	*1951*	*1951*	*1938*	*1951*	*1938*	*1951*	*1938*	*1951*
Necrotauliidae	7	17	1	19	45	2	3	19	45
Prosepididontidae	2	1	—	2	1	—	—	2	1
Rhyacophilidae	30	39	7	364	508	44	71	6	6
Philopotamidae	16	18	3	158	188	17	25	7	7
Hydrophilidae	44	71	10	220	353	28	23	5	5
Stenopsychidae	4	4	—	44	49	2	3	1	1
Polycentropodidae	31	32	9	321	342	58	65	85	84
Psychomyiidae (inkl. Ecnominae)	18	19	6	154	189	41	48	17	17
Xiphocentronidae	—	1	—	—	3	—	—	—	—
Hydropsychidae (inkl. Macronematinae)	44	52	9	595	708	81	85	8	8
Arctopsychidae	3	3	—	19	23	2	4	—	—
Phryganeidae	18	23	8	113	121	42	45	37	40
Limnocentropodidae	1	1	1	4	9	1	1	—	—
Molannidae	4	5	2	23	25	14	14	4	4
Calamoceratidae	11	11	3	92	97	6	5	2	2
Philorheithridae	3	3	—	4	4	—	—	—	—
Odontoceridae	14	14	2	48	57	10	14	6	6
Leptoceridae	45	43	12	485	567	117	141	7	7
Limnephilidae	104	124	34	628	732	258	293	17	19
Beraeidae		7	3		23		10		3
Brachycentridae		7	5		75		17		2
Goeridae		11	7		73		22		3
Helicopsychidae	111	6	2	402	43	86	8	27	4
Lepidostomatidae		39	25		192		16		9
Sericostomatidae		36	9		90		27		4
Thremmidae		4	—		13		—		—
Incertae sedis	7	7	—	7	7	1	1	5	6
Total	517	598	158	3702	4537	810	941	255	283

Das Studium der fossilen Arten wird geschichtlich geschildert. Für die Herkunft der Ordnung wird Tillyard's Theorie bevorzugt.

Ein kurzer Überblick über die Bearbeitung der Faunen der verschiedenen Weltteile lehrt uns, dass besonders Süd-Amerika in dieser Hinsicht noch wenig bekannt ist.

Die Zahl der beschriebenen Arten ist von Ende 1938 bis Ende 1951 um 835 gestiegen. Da in derselben Zeit 131 Artnamen als Synonym verschwanden, sind in diesen 13 Jahren (wovon 5 Kriegsjahre) 966 neue Arten beschrieben worden. Eine nach Familien spezifizierte Aufstellung der Ende 1951 bekannten Genera und Spezies folgt hier mit den Zahlen von 1938 zum Vergleich.

Aus dieser Aufstellung geht eine Zunahme der Genera mit 16% und der Species mit 22% hervor. Leider war es mir nicht möglich eine nochmalige, sehr zeitraubende Zählung z.B. per Ende 1960 vorzunehmen. Trotzdem können wir aus den schon bekannten Zahlen und den Zoological Records der letzten Jahre mit genügender Sicherheit ableiten, dass heute annäherend 700 Genera mit 5500 Arten beschrieben sind. Die Zahl der bekannten fossilen Arten ist in bedeutend geringerem Masse gestiegen (11%) und es ist nicht zu erwarten, dass sich diese Tendenz in der Zukunft ändern wird. Die Erhaltung and das Auffinden von fossilen Insekten ist dafür von zu vielen Zufälligkeiten abhängig.

Wenn ich nun aus der Entwicklung der letzten 200 Jahre einen Schluss ziehen darf, dann möchte ich behaupten, dass die Systematik zwar grosse Fortschritte gemacht hat, die grosse Aufgabe alle Tiere in ein logisch aufgebautes System zu erfassen, jedoch noch nicht vollendet hat. Eine einwandfreie Lösung dieser Aufgabe wird wohl nie möglich sein, aber jede neue Entdeckung, sei es von noch unbekannten rezenten Formen oder von fossilen missing links, wird zur Vervollständigung des Gebildes beitragen. Durch die unermüdliche Arbeit von ungezählten Forschern aus aller Herren Länder sind wir heute jedenfalls so weit, dass wir 400 mal so viel Arten kennen und besser kennen als der Gründer unserer Wissenschaft.

THE GENERA OF ARGENTINE NOCTUINAE (AGROTINAE *SENSU* HMPSN; LEP. HET.)

P. Köhler

Buenos Aires, Argentine

Early revisions of the *Noctuinae* of the Argentine Republic and the neighbouring regions mentioned more than seventy genera. Now, having seen the very important types in the British Museum and in the collections of Paris, Munich and Vienna and using the terminalia characters, it has been possible to restrict the number of names to only twenty three. 14 of these are described as new (1 by Forbes, 1 by Franclemont, 12 by the author) only nine older ones remaining.

Some misused genera like *Lycophotia* Hb., *Epipsilia* Hb., and others, have been eliminated and replaced by new genera not represented elsewhere, which gives a special interest to our south-nearctic *Noctuidae* fauna. (To be published in full by University of Tucuman, Lillo Institution).

SECTION 2.—MORPHOLOGY, ANATOMY, PALAEONTOLOGY

The following papers were read but the authors did not wish for publication in these Proceedings:

Smith, D. S. (U.S.A.). Electron microscopic studies of insect tissues—in retrospect and prospect.

Schmidt, H. (Germany). Über die mikroskopische Anatomie und electronenmikroskopische Struktur des Mitteldarmes der Larve des Hausbockkäfers.

Lacombe, D. (Brazil). The comparative anatomy of the tracheal systems of *Triatoma, Panstrongylus,* and *Rhodnius* (Heteroptera).

Edwards, J. S. (U.S.A.). Ageing in the insect central nervous system.

ELECTRON MICROSCOPY OF INSECT TISSUES

CERTAIN ULTRASTRUCTURAL ASPECTS OF THE PROCESS OF SECRETION IN SALIVARY GLAND CELLS OF INSECT LARVAE

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The salivary glands of the sciarid *Bradysia mycorum* and the chironomid *Smittia parthenogenetica* were studied during the mid-larval period. The larvae of *Bradysia* used had a length of about 6·5 mm, while those of *Smittia* measured 3 mm. In the former the salivary glands are strikingly differentiated into anterior and posterior parts and the large cells of the anterior part were examined. The apical and basal portions of the cells are clearly defined in *Bradysia* as the cells are arranged on the sides of a narrow central duct. This, however, is not the case in *Smittia* where the peripherally situated cells of the globular glands protrude to varying degrees into the large central lumen.

Buffered osmium tetroxide fixed material embedded in Araldite were examined in Siemens Elmiskop I or AE1.EM6. electron microscopes. The sections were stained in a mixture of potassium permanganate and uranyl acetate. A detailed account of the technique as well as observations on the nucleus and nuclear envelope in *Bradysia* are available in earlier publications (2, 3). The ultrastructure of the cytoplasm has also been described (4) and these may be recapitulated briefly for the purposes of this communication.

Both on the apical and basal sides, a layer of cytoplasm surrounds the nucleus and this layer shows abundant profiles of endoplasmic reticulum studded with dense particles. A few profiles of Golgi apparatus and mitochondria are present. On the basal side the rest of the cytoplasm shows similar features, but also contains infoldings of the cell membrane. Another interesting feature concerns the Golgi apparatus, the components of which, unlike those in the apical cytoplasm, appear to be flat sac-like vesicles. The basal surface and its infoldings may enable uptake of raw materials into the cell from the haemolymph in which the glands are free-floating. On the apical side, apart from the layer already described the cytoplasm is differentiated into three zones which may be termed a Golgi-rich zone, a mitochondria-rich zone and finally the brush border at the apical surface. In the Golgi-rich zone endoplasmic reticulum is also abundant and it is inferred that this zone is primarily concerned with the production and condensation of the secretory material. The brush border seems most likely to be concerned with the discharge of the secretory products into the gland duct. In *Smittia* apart from the apical brush border and the basal surface with its infoldings, the rest of the cytoplasm is not clearly differentiated into zones (Jurand and Jacob, unpublished). It may be that the larval stages studied in the two species are not in comparable or identical stages of development.

Mention was made in *Bradysia* of the different appearance of the Golgi apparatus in the apical and basal cytoplasm. Golgi of the type in basal cytoplasm were very seldom found in the apical cytoplasm. The main components of this organelle in the Golgi-rich zone are large spherical vacuoles and smaller vesicles and clusters of very small dense granules which measure 200 to 500 Å in diameter. The granules are a constant and characteristic feature and a careful study has suggested that they form a connecting link between endoplasmic reticulum on one hand and the Golgi apparatus on the other. On rare occasions the granules appeared to lie inside the cavity of the endoplasmic reticulum and in many instances they gave the impression of budding off from the endoplasmic reticulum. At the other end, i.e. at the Golgi apparatus, besides the numerous free lying granules, some granules could be seen at the walls of the Golgi vesicles and vacuoles into which they presumably discharge their contents. The large vacuoles then probably migrate to the apical surface as secretory vacuoles and are discharged from the cell.

Similar observations which suggest close relationship between endoplasmic reticulum and Golgi apparatus through the interlinking dense granules have been made in *Smittia* as well (Jurand and Jacob, unpublished). But Golgi apparatus consisting mainly of parallel arrays of lamellae have been found in many instances in the apical cytoplasm to the exclusion of the type so far described. Some of the lamellae are closely packed, but others seem to bound distended cisternae. The appearance of some of the latter as well as the occurrence of closely associated vesicles prompt the suggestion that the vesicles are pinched off from the enlarged Golgi cisternae. A few large vacuoles are also noticed at these sites. The Golgi apparatus under discussion lie in cytoplasm which is more or less clear of, or is only sparsely surrounded by, endoplasmic reticulum.

The Golgi apparatus thus appears in two or three different morphological configurations in the actively secreting salivary gland cells of the insect larvae studied. These differences may be indicative of different functional roles. In the type which shows intimate association with the endoplasmic reticulum, the Golgi system may serve as an aggregation centre for protein secretory products (represented perhaps by the dense granules) synthesized by ribonucleoprotein particles or ribosomes and transported to the Golgi site through the internal phase of the endoplasmic reticulum as has been suggested by Palade and his collaborators (1).

In the other morphological type the Golgi apparatus may serve as a centre of synthesis of non-protein secretory material such as complex carbohydrates by enzyme systems on its membranes.

Evidence for differing functional roles of Golgi apparatus in secretory process abound in literature (5) and with the recent development of reliable techniques for electron microscope autoradiography, it should be possible to check if a particular morphological form of the Golgi apparatus can be related to a particular function. From our limited studies in two arbitrarily chosen larval stages it is not clear if one morphological type changes to the other, but indications are that one type predominates in the apical cytoplasm at a given time.

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THE ULTRASTRUCTURE OF THE LEPIDOPTERAN STRETCH RECEPTOR

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The fine structure of the abdominal stretch receptor of *Antheraea pernyi* is described in larval receptors fixed in 0·6% potassium permanganate, and pupal receptors fixed in glutaraldehyde.

The receptor consists of a multipolar neurone, the dendrites of which are associated with a tube of connective tissue, the fibre tract, that is attached to the edge of a single specialised muscle fibre.

The fibre tract consists of a tube of amorphous connective tissue (basement membrane material) in which there lie connective tissue fibres forming an inner ring. At the junction of the fibre tract with the muscle fibre, there are large bundles of connective tissue fibres, the fibre bundles, which run longitudinally for most of the length of the receptor. Towards the ends of the receptor the number of these bundles decreases until eventually at the ends of the receptor they peter out altogether. Within the fibre bundles, the connective tissue fibrils show a tendency to adhere together, so that dense accumulations of compound fibres are formed, looking in cross section like irregular dark areas. The degree of condensation of fibrils differs between the bundles so that some bundles appear much darker than others. In many fibre bundles can be seen micro tubules. These tubules also occur to a lesser extent amongst the connective tissue fibrils of the inner ring. The lumen of the fibre tract is filled partly by the cytoplasm of the tract cell and partly by the dendrites from the neurone. The tract cell contains a few mitochondria and a well developed internal membrane system. In this cell, at the central region of the receptor, lies the large tract nucleus or minor giant nucleus. It is likely that the tract cell is responsible for the formation of the ring of connective tissue fibres and the fibre bundles.

The multipolar sensory neurone is ensheathed by numerous wrappings of Schwann cells. Two, three or four main dendrites run from the cell body, enter the fibre tract, and run longitudinally inside it parallel with and adjacent to the fibre bundles. Throughout their entire length the dendrites branch repeatedly to give rise to smaller dendrites which are associated with the fibre bundles. Although the dendrites are surrounded by Schwann cells, the tips of the final terminations are left bare and are either adpressed to the surface of the fibre bundles or penetrate the bundles.

The muscular component consists of a single muscle cell whose large nucleus (major giant) is located in a central swelling. The perinuclear cytoplasm, or cytoplasmic core, which contains mitochondria and granules but no myofibrils, continues as a spindle-shaped extension which runs in both directions along the centre of the muscle fibre almost in some cases to the ends of the receptor. The myofibrils are irregular in shape and surrounded by the sarcoplasmic reticulum. A transverse tubular system is present and this is continuous in places with the plasma membrane. Motor endings are found along the entire length of the muscle even in the central swelling where the myofibrils are very sparse.

ULTRASTRUCTURE DE LA GLANDE STERNALE CHEZ LE TERMITE *CALOTERMES FLAVICOLLIS*

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Cette glande, située à la partie antérieure du 5ème sternite abdominal, est un coussinet épidermique formé d'une seule assise de cellules en continuité avec l'épiderme banal. D'après Lüscher et Müller, et d'après Stuart, c'est de là qu'émane la sécrétion odorante dont se servent les Termites pour marquer leurs pistes.

Les cellules reposent sur une membrane basale très épaissie (jusqu'à $1{\cdot}5\mu$) formée de fibres parallèles d'environ 80 Å de diamètre. La cuticule recouvrant la glande est épaissie. Ses caractères de colorabilité sont modifiés; elle n'est percée d'aucun pore excréteur.

La glande est formée de deux catégories de cellules: cellules glandulaires et cellules intercalaires; toutes deux reposent sur la basale, mais seules les cellules intercalaires atteignent la cuticule. Dans la région basale, les membranes des cellules contiguës sont simplement accolées, mais dans la région apicale les cellules intercalaires sont unies par un système complexe et très développé de différenciations membranaires (zonules d'adhésion et desmosomes cloisonnés).

Les cellules glandulaires sont caractérisées par de nombreuses inclusions sphériques, limitées par une membrane simple, à contenu apparemment homogène et de faible densité aux électrons; leur diamètre avoisine souvent 1μ, mais elles peuvent confluer en vésicules parfois très volumineuses. Les mitochondries, très polymorphes, montrent souvent un gonflement qui repousse les crêtes vers la périphérie. L'appareil de Golgi est très peu développé. Il n'y a pas d'ergastoplasme organisé, mais seulement des grains de Palade. On observe enfin des "vacuoles" à contour irrégulier et contenu clair. Le feuillet externe de la membrane nucléaire s'écarte par endroits, et l'espace périnucléaire vient faire hernie dans le cytoplasme.

Les cellules intercalaires, étroites dans leurs parties basale et moyenne, s'étalent sous la cuticule où leur surface apicale présente une différenciation remarquable: elle est garnie d'un revêtement dense de microvillosités rappelant une bordure en brosse. Les microvilli ont un diamètre un peu inférieur à $0{\cdot}1\mu$; leur longueur, difficile à apprécier en raison de leur trajet sinueux, peut dépasser 1μ; leur structure n'est pas homogène: les coupes transversales révèlent l'existence d'un axe central entouré d'une couronne de fibrilles. Les mitochondries présentent le même polymorphisme et les mêmes aspects de gonflement que ceux des cellules glandulaires; elles sont souvent allongées suivant l'axe de la cellule; l'espace périnucléaire montre les mêmes figures de dilatation. En revanche, l'aspect du cytoplasme est très différent: absence des inclusions sphériques, présence de fibres tubulaires ($d = 120$ Å) et d'un système de saccules. Ces saccules, très aplatis, (200 à 400 Å d'épaisseur), allongés suivant l'axe de la cellule, s'étendent souvent le long des membranes latérales, ou bien s'empilent, évoquant un peu l'aspect des corps de Golgi. On retrouve des "vacuoles" ayant la même apparence que celle des cellules glandulaires, mais plus développées. Certaines images suggèrent un rapport de ces vacuoles avec les évaginations de l'espace périnucléaire, le système des saccules et la membrane cellulaire.

THE ULTRASTRUCTURE OF THE GUT EPITHELIUM OF MOSQUITOES (DIPTERA)

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The mosquito midgut epithelium is a layer of columnar to cuboidal cells with, by light microscopy, a striated border on the surface lining the gut lumen and a nucleus, and nucleolus, as the prominent features within each cell. When a blood meal is taken, the midgut distends greatly, the epithelium becomes stretched and flattened and a fine membrane, the peritrophic

membrane, forms round the blood-mass within the midgut lumen. Earlier workers demonstrated protease activity in the midgut 1 or 2 hours after the ingestion of blood by *Aedes aegypti* and a rising amino-nitrogen content in the whole mosquito from 3 hours up to 24 hours, the limit of the study. The timing of these physiological manifestations of digestion and absorption indicates a rather slow initial activity by the gut cells in response to the blood meal.

Electron microscopical study of the midgut of *Aedes aegypti* (1) confirms that the epithelium is of nucleated cells and, in each cell, a layer of mitochondria lies close to the luminal surface membrane. This surface is thrown into numerous elongate microvilli containing extensions of the cytoplasmic substance to form the striated border of light microscopy. Mitochondria are also numerous towards the haemocoelic aspect of the cell, lying between long invaginations, or septa, of the basal cell membrane. Thus, mitochondria are particularly localised at the two active surfaces of the cell.

The cytoplasm of the mosquito gut cell is cytochemically positive for RNA (3, 1) and by electron microscopy is particulate, consisting by analogy (5) of ribosomes of ribonucleic acid and protein (RNP), sites of protein synthesis (2). A further RNA-positive component in the cytoplasm takes the form of whorls or "fingerprints", as seen in sections, of granular endoplasmic reticulum, some approaching the size of the nucleus. The RNA-component resides in the particles on the cytoplasmic surface of this canalicular system. Golgi complexes are fairly numerous, to some extent closer to the nucleus than otherwise, and possibly intercommunicating with the endoplasmic reticulum system.

Bertram and Bird (1) conceive the whorls to be, in three dimensional concept, subglobular in form and composed of arrangements of long but tightly-coiled strap-like vesicles of the endoplasmic reticulum. After ingestion of a blood meal, the whorls uncoil until, during the main phase of digestion, the endoplasmic reticulum ramifies widely throughout the cytoplasm. After digestion is completed, the endoplasmic reticulum returns to its former coiled disposition. This transient ramification of the endoplasmic reticulum occurred only with a blood meal and not in starvation, nor on a diet of water or of sugar. Similar cytoplasmic components, including the whorls of endoplasmic reticulum and their changes to dispersed ramifications during blood digestion, occur also in *Aedes togoi* and have since been observed in *Anopheles stephensi* and *A. gambiae*, although there are differences between species of mosquito. On analogy with endoplasmic reticulum whorls in guinea pig pancreatic cells (4)—which, however, do not unfold during metabolic activity—it appears that the dispersed phase in the mosquito gut cell may be associated with segregation and transportation of proteolytic enzymes required for blood digestion. Roth and Porter (6) suggest that yolk synthesis begins in these gut cells.

Within half-an-hour of taking a blood meal, and when the endoplasmic reticulum whorls have barely begun to unfold, a copious secretion appears between the microvilli to envelop the blood-mass. This secretion is interpreted as the peritrophic membrane; it is a granular layer rather than a complex laminated membrane and is well formed within 15 hours of feeding. The peritrophic membrane may simply be a zone of interaction between blood and enzymes which retains a persisting identity as an enveloping film.

An interesting point is the apparent similarity of cell structure throughout the mosquito midgut; there is so far no conclusive evidence that cells of specialised function occur in the gut, at least not numerously nor segregated in zones. The same cells appear to accomplish secretion to digest the blood in the lumen, absorption of the products and their passage to the basal surface and into the haemocoele, besides maintaining their own intrinsic metabolism. Some clear vacuoles in freshly-fed mosquitoes may represent a transport mechanism and, particularly in older mosquitoes, complex vacuolar structures are as yet not understood.

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THE REGENERATIVE CYCLE IN THE MIDGUT EPITHELIUM OF *PODURA AQUATICA* L. (COLLEMBOLA, PODURIDAE) AND A POSSIBLE MODE OF EXCRETION

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Electron microscopical observations confirm the periodic sloughing and regeneration of the midgut epithelium in sequence with the moulting cycle, as noted by earlier workers (5, 3, 2), and further aid the interpretation of the sequence of events during the regenerative cycle.

STAGE 1. EARLY INTERMOULT. Two cell types, columnar epithelial and cuboidal regenerative cells, occur in the epithelium. The regenerative cells occur singly or in groups at the base of the epithelium, above the basement membrane. These 4μ cells with relatively clear 3μ nuclei have relatively dense cytoplasm filled mainly with mitochondria. The epithelial cells are 6-9μ deep and 7-8μ wide, with relatively dense 3-4μ nuclei. Beneath an apical brush border of microvilli 1μ long and 100mμ in diameter, smooth-walled vesicles 100mμ in diameter occur and some appear to open to the lumen between the microvilli, suggesting a possible mode of enzyme secretion. The cytoplasm contains electron-dense granules 0·5μ in diameter in 0·7-1·5μ vesicles, mainly at the base of the cell. Material within the vesicles appears to come from the cytoplasm and to be added to the granules concentrically.

STAGE 2. LATER INTERMOULT. The granules are 1μ in diameter and their vesicles 2-3μ.

STAGE 3. VERY EARLY PREMOULT. The regenerative cells have divided and formed new regenerative and epithelial cells, squatter than the old ones, below the old epithelial cells, which are more fully filled with the 1μ granules and their 2-3μ vesicles, giving their nuclei irregular outlines.

STAGE 4. EARLY PREMOULT. The new regenerative and epithelial cells are rounding off towards full size and a space is evident between new and old epithelial cells. In the old epithelial cells the vesicles are larger, 3-4μ by 2-3μ, and the granules have concentric laminae. The nuclei are very irregular. Secretion droplets are forming and emptying into the large vesicles. Numerous smaller vesicles 150μ in diameter are present.

STAGE 5. MID PREMOULT. The old epithelial cells are now almost filled with large vesicles and their granules, and some nuclei are beginning to disintegrate. Microvilli are developing on the new epithelial cells, which are now columnar and already contain small electron-dense granules 200mμ in diameter.

STAGE 6. POSTMOULT. The old cells are being digested. The concentric granules remain in the gut lumen for a short period only. The new epithelial cells are complete and the granules and their vesicles are already growing.

This sequence of events thus culminates with the voiding of numerous granules, as well as other vesicular material. The conclusion of Folsom and Welles (3) that this is a form of excretion seems to be supported by the formation in Malpighian tubules of concentric granules in *Gryllus domesticus* (1) and *Rhodnius prolixus* (6) and of brochosomes in *Macrosteles fascifrons* (4), though whether or not the granules in *Podura aquatica* are uratic spheres requires further investigation. These granules further indicate that Malpighian tubules may have arisen from the midgut.

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PALAEONTOLOGY AND EVOLUTIONARY MORPHOLOGY

THE ECOLOGY OF PERMIAN INSECTS

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Very rich localities of Lower Permian fossil insects were found in the Boskovice furrow in Moravia. In Permo-Carboniferous it was a deep intermontane depression, with lakes at the bottom and bordered and sheltered by the surrounding hills. The close proximity of hills allows knowledge of flora and fauna of the highland in Permian, as well as in Carboniferous times.

Because insects are closely connected with flora, the advanced "Permian" types of insects most probably lived on xerophilous plants in highlands possibly also near the Carboniferous swamps, at least during the Stephanian. From this point of view, the well-known abrupt change of entomofauna between Carboniferous and Permian is only seemingly sudden, because from Carboniferous almost only lowland insects are known. During the Lower Permian, with the continuing aridisation, the "Permian" advanced insects migrated into the lowlands together with xcrophilous plants.

In the Boskovice furrow, the warm temperate climate in Lower Permian superseded gradually the subtropical climate of the Upper Carboniferous and twenty orders of insects, very rich in species, were found.

The author has studied in detail the family Liomopteridae of the order Paraplecoptera. As in Plecoptera, there are specimens with broad fore wings and rich venation, little accommodated for flying and also with narrower fore wings and poor venation, better accommodated for flying. The rich fauna of liomopterids has been described from the Permian of Kansas, Kuznetzk Basin and Moravia. In Kansas the climate was fairly warm. The insects inhabited only a more humid portion of the semi-arid lowland. Among liomopterids, both small specimens with the length of wings under 10 mm and large ones over 30 mm, as well as those with narrow wings, are lacking. In the Kuznetzk Basin the climate was colder and continental and there were no hills. Large specimens with fore wings 26-50 mm long are more abundant than small specimens 8-13 mm; specimens with narrow wings are lacking. In Moravia, there was a warm, temperate climate with hills close by. Many small specimens under 10 mm have been found, chiefly with narrow fore wings, well adapted for flying. Large specimens over 30 mm are lacking. According to the very close morphological analogy with recent Plecoptera, it seems possible that some of the small and particularly of the narrow-winged liomopterids could derive from the submontane biotopes, whilst the broad-winged liomopterids lived probably in lowland biotopes. This hypothesis is supported by the fact that the bodies of narrow-winged specimens are often complete, evidently transported by the wind and that they occur in layers with aeolian material. It is of great interest that the very large broadly winged specimens of liomopterids have not yet been described from the warmer regions (CSSR, Kansas). But as the abundant specimens of Tschekarde (East Europe, U.S.S.R.) are not yet published, no conclusion can so far be drawn.

Interesting morphological studies have been done of the highly specialised hemimetabolous order Protelytroptera. Of this order again, most primitive specimens with slightly convex elytra appear in Moravia. Very peculiar protelytrids with flattened elytra of specialised as well as of primitive type were also found. The flattening of elytra is probably a functional accommodation for the life in crevices, of only little significance for the phylogeny of the order. Similar modifications are known in modern beetles.

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SOME THOUGHTS CONCERNING THE INSECTS OF THE BALTIC AMBER

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Baltic amber is a fossil resin of early Oligocene (or late Eocene) age, distinguishable from other fossil resins by high content (about 5%) of succinic acid and by its infra-red absorption spectrum. Fossil insects in it are often very well preserved; nearly all of them are small, as is the case with the catch of modern sticky traps on tree-trunks. The best represented groups are Diptera-Nematocera, Hymenoptera-Parasitica, Coleoptera and Homoptera. Study of amber insects has hitherto been very partial and imperfect, by no means commensurate with the scientific interest and importance of this fauna. Amber fossils should be studied with the greatest care by leading specialists on the world faunas in the various groups.

The amber flora and fauna generally indicate a warm temperate to subtropical humid climate. In critically revised groups, about half the genera in the amber are extinct. The living species of genera represented in the amber often occur in S.E. Asia, but some are in America, Australia, S. Africa, and even Europe. There is very little knowledge yet of regional insect faunas in the early Tertiary, but distributions would probably be comparable with those of mammals of the time. Amber fossils should *not* be discussed in terms of present-day zoogeographical regions.

The amber trade having been strictly commercial, and good insect inclusions having commanded high prices from collectors, faked inclusions are likely to have been produced and sold; where amber inclusions seem to be conspecific with modern (and especially, modern European) insects, the specimens should be critically tested for faking.

Wheeler (1914) in his study of amber ants, may have been deceived by artificial inclusions of modern European ants in amber, e.g. *Formica flori* and *Lasius schiefferdeckeri.* His (and Huxley's) conclusion that ants had reached their evolutionary limits by the early Tertiary era rests on this suspect evidence and is not supported by other amber fossils.

The amber Trichoptera appear to lack entirely the dominant modern European family Limnophilidae (4) and the Psocoptera (Enderlein 1911)likewise lack many common modern European genera. The Syrphidae exhibit similar features (2); *Syrphus* and its close allies are lacking, as are Eristalinae and true Volucellinae—most of the fossils are rather primitive types of Syrphinae and Cheilosiinae.

Among the Coleoptera, the ant-parasitic Paussidae of the amber (1, 5) are entirely devoid of Paussinae, the most advanced subfamily and the only one represented in the modern Palaearctic fauna. According to Schedl (3), the Scolytidae of the amber are all Hylesininae or very primitive Ipinae, there are no Scolytinae, Platypodinae or higher Ipinae such as *Ips, Orthotomicus, Pityogenes or Pityophthorus.* Of the Chrysomelidae-Hispinae, Uhmann describes 2 extinct genera from the amber, constituting an extinct tribe Oposispini; he considers the nearest relatives of Oposispini to be Indo-Malayan.

I have examined some Cleridae from the Baltic Amber; so far, I have seen no species of the dominant modern European genera *Tillus*, *Opilo*, *Thanasimus*, *Trichodes* or *Necrobia.* I have described one extinct genus of Tillinae, related to Indo-Malayan types, and have distinguished two genera of Clerinae, not yet satisfactorily identified.

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THE ORIGIN OF INSECT FLIGHT: SOME IMPLICATIONS OF RECENT FINDINGS FROM PALAEOCLIMATOLOGY AND LOCUST MIGRATION

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Evidence on the mechanism of locust migration (3) has directed attention to the marked survival value, in arid areas, of even undirected flight-activity, since the resulting down-wind displacement must, on balance, be towards zones of convergent surface winds; and such convergence is essential for the production of significant rainfall. In semi-arid and desert areas, flight without systematic orientation can thus make possible the colonisation and exploitation of the ephemeral but extensive vegetation which characteristically follows the erratic rains of these areas. Even some of the most arid areas of Arabia and the Sahara are known to experience from time to time rain in quantities of the order of centimetres; and such exceptional rains have repeatedly been associated with an influx of locusts.

Furthermore, the arid and semi-arid areas are also characterised by particularly vigorous thermal up-currents, developing regularly by day over the heated ground and rising at speeds of several metres per second (2). These currents are accordingly capable of lifting any airborne material or organism with a sinking-speed, relative to the air, less than these rates of ascent (1); the sinking-speed of a gliding locust, for example, flying without flapping, is about one metre per second (2, 5).

It is therefore suggested that even the initial stages in the evolution of flight, by early insects unable to remain airborne by their own efforts for more than a few seconds of descent and as yet incapable of any controlled aerial manoeuvre, could have been of positive survival value under the conditions of the arid areas.

There is, moreover, reason to believe that such conditions have existed since geologically remote times, not only in general terms but in relation to particular global weather-features. One of these features, a quasi-permanent zone of convergent winds which has been found to dominate the movements and distribution of locusts during much of the year, is the Inter-Tropical Convergence Zone, between opposing wind-currents (such as the trade-winds) originating on opposite sides of the equator in the subtropical anticyclonic belts associated with the great deserts. These wind-systems are major features of the general circulation of the atmosphere, deriving their energy from the sun's radiation; they are manifested in both northern and southern hemispheres, despite differences in distribution of land and sea; and on geophysical grounds they are likely to have existed on this same basic plan, though with fluctuations in the relative extent of its different features, since far back into geological time. Furthermore, independent direct evidence on this latter point has recently begun to become available, in the form of fossil *barchan* sand-dunes found to indicate persistent easterly "trade-winds" in appropriate Permo-Carboniferous latitudes (4). Finally, the very poverty of the early fossil record of insects would be consistent with the early stages in the evolution of flight having occurred under arid conditions in which the possibilities of fossilisation were minimal.

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CRANIAL DEVELOPMENT IN THE HEMIPTERA

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The modern Hemiptera (Orders Homoptera and Heteroptera) have entognathous heads modified for piercing and sucking rather than biting and chewing. Their mandibles and maxillae form long, slender stylets whose bases are concealed by the loral and maxillary plates, and endoskeletal food and salivary pumps are present.

A possible explanation of how the skeletal parts of the ancestral Hemipteran cranium could have arisen from a basic Pterygote plan is here summarized; it is discussed in more detail in a previous paper (3). This theory may be broken down into four idealised phylogenetic stages, at least partially reflected in the ontogeny of modern Hemiptera.

STAGE 1: The mandibles and maxillae of an ancestral Pterygote head developed into stylets rather than biting appendages. Meanwhile the regions below the tentorial pits became elongated.

STAGE 2: To support and protect the narrow stylet bases, and to provide origins for the stylet protractor muscles, the loral and maxillary plates were formed. The former arose from lateral swellings of the hypopharynx (5); the latter originated from the genal-postgenal region. DuPorte (1) has proposed that this region has descended, in advanced mandibulates, below the level of the tentorial pits, carrying with it the attached appendages. I believe that in Hemiptera the genae and postgenae descended below the tentorial pits as a lobe, lateral to the bases of the stylets, which remained at their original level. The inner wall of the lobe formed the endoskeletal lamina maxillaris, while the outer wall became the maxillary plate. Embryological observations indicate that the latter is a non-appendicular derivation (4).

STAGE 3: The food and salivary pumps arose from the lateral closure of the cibarium and salivarium respectively (2, 5). As the cibarium closed laterally, the clypeoloral clefts became increasingly obliterated below the anterior tentorial pits; this is the reverse of the theory proposed by Spooner (6). The part of the clypeoloral cleft which remains varies in length from one modern Hemipteran to the next.

STAGE 4: The stylet bases became enclosed in separate endoskeletal sacs, providing separate muscle insertions and allowing independent movement of the stylets. In previous stages the stylets lay in a common cavity between the lamina maxillaris and hypopharynx; in Stage 4 this cavity was subdivided into maxillary and mandibular sacs by a coming together of the lamina maxillaris and hypopharynx around the stylet bases. During this process the external clefts between the maxillary plate and hypopharynx became closed off, the closure beginning at the tentorial pits and progressing downwards to a variable extent. The walls of the stylet sacs produced the maxillary and mandibular levers.

Modern Homoptera possess Stage 4 heads. A tentorium is present, the head capsule is open posteriorly, and the external clefts between sclerites are generally not as extensively closed as in Heteroptera. The Heteropteran cranium is more advanced; the tentorium is absent, the primitive clefts are more extensively obliterated, and the head capsule is closed posteriorly by a sclerotised hypopharyngeal or postgenal plate.

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ANATOMY AND HISTOLOGY

LE POLYMORPHISME ALAIRE CHEZ LES BLATTES (INSECTES DICTYOPTERES)

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Les Blattes présentent au point de vue polymorphisme alaire un intérêt exceptionnel. On trouve en effet chez ces Insectes, non seulement des espèces à ailes normalement développées et des aptères, mais encore toute une série de types intermédiaires. Avant d'entreprendre une étude du déterminisme de cette réduction alaire, il était nécessaire d'en tenter l'analyse morphologique et anatomique. C'est dans ce but que nous avons étudié l'organogenèse des nerfs et des trachées de l'aile d'un certain nombre de Blattes. Nous ne donnons ici que quelques exemples destinés à mettre en relief les étapes marquantes de ce phénomène.

Chez une blatte à ailes normalement développées, les ébauches alaires méso ou méta-thoraciques subissent, lors de la mue imaginale:

—une torsion vers l'arrière dans un plan horizontal qui amène l'axe général de l'aile, défini par l'orientation de la trachée radiale, parallèle à l'axe du corps.
—la formation d'une base alaire mobile par le jeu de sclérites alaires.
—un allongement et un élargissement général de l'ébauche alaire.
—une scission entre le champ notal et le champ anal.

L'un de ces 4 phénomènes peut, chez les *Blattidae*, disparaître ou se réaliser d'une manière atténuée, ce qui se traduit par un polymorphisme alaire spécifique.

La comparaison des ailes de *Blatta orientalis* à celles d'une Blatte à organes de vol bien développés, telle que *Periplaneta americana*, permet de constater que la différence majeure réside dans la disparition distale de l'aile. Cette réduction touche davantage l'aile métathoracique que la mésothoracique et elle est plus importante chez la femelle que chez le mâle, ce qui détermine un dimorphisme sexuel, (cas fréquent dans cet ordre d'Insecte).

Chez une blatte microptère, telle que *Loboptera decipiens*, seule l'ébauche alaire mésothoracique va subir un début de métamorphose à la mue imaginale. Cela se traduira, entre autre, par la scission champ notal-ébauche alaire et la formation partielle des sclérites antérieurs. Mais, alors que la séparation s'établit chez les Blattes brachyptères entre le champ notal et le champ anal, elle s'effectue chez *Loboptera* entre le champ cubital et le champ anal; ce dernier étant reporté sur le champ notal. (Nous pensons que cette élimination du champ anal caractérise le microptérisme de beaucoup d'Insectes, ainsi que de nombreux exemples semblent le prouver: absence de champ anal chez les *Psyllipsocus ramburi* microptère, de nerf anal dans les balanciers de *Tipula paludosa*).

L'absence d'évolution morphologique de l'ébauche alaire métathoracique de *Loboptera*, lors de la mue imaginale, nous conduit au cas extrème de la réduction de l'aile chez les *Blattidae:* celui des Blattes dites "aptères". Celles-ci possédent un véritable *développement amétabole* acquis sans doute secondairement (*Gromphadorhina laevigata*). Il est important de noter que, mis à part quelques différences telles que le développement de la trachée costale, la diminution du nombre de trachées secondaires et la réduction du groupe de trachées cubito-anales représenté par une seule trachée (parfois bifurquée), ces Insectes possédent les mêmes nerfs et les mêmes trachées alaires que des blattes normalement ailées. Leur aptérisme apparaît ainsi comme fondamentalement différent de celui de certains insectes (Siphonaptères) et c'est pourquoi nous avons proposé le nom de *subaptère*: Insecte adulte à ébauches alaires de type larvaire, pour définir ce cas extrême de la réduction de l'aile chez les Blattes.

ANATOMICAL AND HISTOLOGICAL STUDIES OF THE RETROCEREBRAL COMPLEX OF *PERIPLANETA AMERICANA* (L.) (DICTYOPTERA)

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A modified Wigglesworth's (3) fixative that consists of 1% osmium, 0·1 M trichloroacetic acid, and 0·2 M potassium chloride enabled light-microscopic investigations to define clearly cell boundaries in the retrocerebral complex of ten-week-old male adults of *Periplaneta americana* (L.). As it was possible to stain for neurosecretion after osmium fixation, a better perspective of the histology of the corpora cardiaca was obtained.

Studies on the innervation of the corpora cardiaca from the brain in the male revealed the union of a slender branch from the NCC I (internal *nervus corporis cardiaci* from the *pars intercerebralis* (1, 4)) with the NCC III (*nervus corporis cardiaci* from the tritocerebrum (4)) before the NCC III enters the corpus cardiacum. There were neurosecretory granules in the NCC I, the NCC III, and in the branch between them. As the NCC I and the NCC III originate from different regions of the brain, a union between them may be significant to the functioning of the retrocerebral complex.

The posterior cardium tissue of the two *nervi cardiostomatogastrici* (NCS) unites with the hypocerebral ganglion and crosses on its dorsal side. Contrary to Willey's opinion (4), our material showed axons full of neurosecretory granules and the larger axons of the NCS crossing with this tissue.

The cephalodorsal glandular region of the corpus cardiacum, which lies above the basal nerve (the combined axonal tracts from the brain leading to the corpora allata and hypocerebral ganglion) and which extends caudally to where the basal nerve branches into the NCA I (*nervus corporis allati* I) and the NCS, appears as a highly osmiophilic "sac". The osmiophila of the "sac" is dependent on the highly osmiophilic neurosecretory granules of brain origin and on the osmiophilic intrinsic cells that are confined to this region.

Five types of cells appear to occur in the corpora cardiaca of the male: two types of intrinsic cells confined to the osmiophilic glandular "sac", and separated by their difference in cytoplasmic volume in relation to their nuclear size and in osmiophilia; osmiophobic ganglion-like cells concentrated mainly just caudally to the "sac", where the basal nerve branches into the NCA I and the NCS, but with a few extended along the basal nerve and the NCS; a few "inclusion" cells with a process, which contain one or two large osmiophilic (phloxinophilic) inclusions (about four microns in diameter) in their osmiophobic perikarya, occurring in the NCS and in the commissural region of the hypocerebral ganglion; and osmiophobic glia-like cells with irregular shaped nuclei found throughout the corpus cardiacum. As sheath cells of the corpora cardiaca appear glia-like, they were grouped with this fifth cell-type. However, further studies may reveal them to be of a perineurium nature (2). Until evidence to the contrary is forthcoming, glandular intrinsic cells with the larger volume of cytoplasm that possess either varied numbers of processes or whose cytoplasm varies slightly in osmiophilia are considered to be one type of cell.

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HISTOLOGICAL AND HISTOCHEMICAL STUDIES ON THE BRAIN OF THE WATER-BEETLE *DYTISCUS MARGINALIS*

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The brain is surrounded by a single-layered epithelium with unipolar nerve cells beneath, which lack anastomoses. Inside the nerve cells there is a neuropile consisting of nerve fibres forming plexuses in synaptic connection. Peculiar centres are the mushroom-body stalk, the trabacle, the backward arching stalk, the central body, the optic ganglia and the olfactory glomeruli.

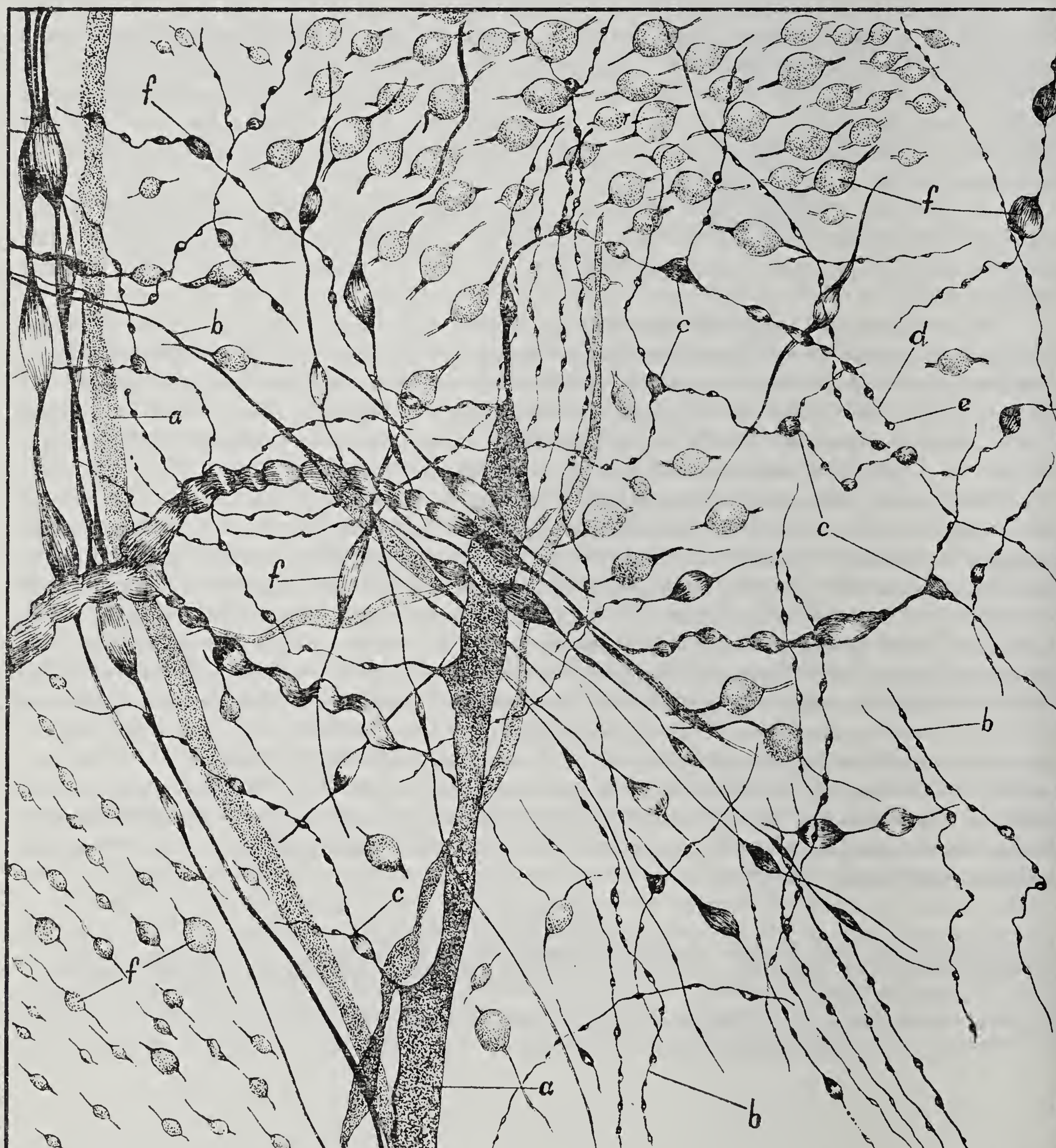

Fig. 1. *Dytiscus marginalis:* The fibre-substance of the brain. (*a*) thick nerve fibre, (*b*) thin nerve fibre, (*c*) branching, (*d*) end-fibre, (*e*) ending, (*f*) varices. Jabonero's silver carbonate impregnation method. Microscopic magnification 1600 ×.

The mushroom-body stalk consists of a great number of varicose nerve fibres in intimate contact with the thick fibres coming via the oesophageal connectivum. The nerve fibres of the trabacle are surrounded by a cortical plexus originating from the giant fibres coming from the infra-oesophageal ganglion. The backward arching stalk shows a structure similar to the trabacle (fig. 1). The central body consists of fine nerve fibres, some passing into the dorsal part of the body and ending free near the surface. The optic ganglia are nerve fibre plexuses surrounded by a cortex consisting of a layer of unipolar nerve cells. The fibres come partly from the eye, partly from the ganglia; the former form synapses with the latter. The olfactory glomeruli are of longish, rounded plexuses within the inferior and exterior corner of the deutrocerebrum. Their nerve fibres, originating partly from the sensory cells of the antenna partly from the cells at the base of the medial mushroom-body, form a long contact synapses.

In the protocerebrum three cell groups were found whose members show neurosecretory activity. The first group is located in pars intercerebralis, the second beside the medial mushroom-body and the third at the base of the lateral mushroom-body. The cells of the first group are large, in the cell-body neurosecretum granules could be seen appearing red, stained with paraldehyde fuchsin, dark violet, pale violet or red with chrom-haematoxilin floxin (fig. 2).

The production of the neurosecretum is the highest at noon, at mid-night and at 2 a.m. The productivity of the cells is increased by ultrasonic and electronic excitation and still more by strong electric light. The neurosecretum is probably a glycoproteid showing different reactions in the different transformation phases.

The cells of the second group are of variable size, their granules could be stained only with paraldehyde fuchsin and they do not leave the cell-body.

Those of the third group are all of smaller size, their granules pass from the cell-body and form thin columns between the cells or the nerve fibres.

FIG. 2. *Dytiscus marginalis:* Neurosecretory cell groups in pars intercerebralis of the protocerebrum. (*a*) epithel-cell, (*b*) epithel cell-nucleus, (*c*) neurosecretory-cell, (*d*) nucleus, (*e*) neuro-secret, (*f*) pathway, (*g*) nerve fibres. Stained with chrom-haematoxilin floxin. Microscopic magnification 300 ×.

ETUDE HISTOLOGIQUE DES GONADES D'INTERSEXUES TRIPLOIDES CHEZ *DROSOPHILA MELANOGASTER* MEIG.

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Je limiterai cet exposé préliminaire à l'étude des gonades des catégories 1 et 2, déjà définies (1). Ces glandes ont, malgré leur morphologie variable, la couleur uniformément jaune des testicules.

Les gonades ont été fixées au Helly ou au Bouin aqueux et les coupes colorées au Feulgen-vert lumière ou à l'Hemalun-erythrosine-orangé G.

Structure des Gonades de la Categorie 1 (Appareil mâle complet)

La paroi du testicule est normale (tuniques externe et interne).

L'apex de la gonade est toujours occupé par des spermatogonies qui s'organisent en groupes allongés transversalement, au fur et à mesure qu'elles s'éloignent de l'extrèmité du testicule. Puis les spermatogonies font place à des spermatocytes de premier ordre qui entrent en phase d'accroissement.

Quelques cellules germinales dégénèrent, comme elles dégénèrent dans les testicules de mâles diploïdes. Ainsi, l'évolution des cellules germinales est jusqu'à présent identique à celle observée dans les testicules de mâles.

Par contre la structure des testicules d'interséxués âgés de plusieurs jours est totalement différente de celle des testicules de mâles de même âge. En effet, chez ces derniers, il n'y a presque plus de spermatocytes, mais surtout des spermatides et des spermatozoïdes. Au contraire, ici, les spermatocytes remplissent plus de la moitié apicale du testicule. Le reste de la gonade est occupé par diverses formes de dégénérescence, que l'on ne trouve jamais dans les testicules de mâles. Une de ces formes est d'un grand intérêt: il s'agit d'un magma cytoplasmique peu colorable, où ne se distingue aucune structure, sinon des plages chromosomiques. Ces plages correspondent à des figures nucléaires de diacinèse, parfois peut-être à des métaphases ou à des anaphases de division hétérotypique.

Je n'ai pu déceler de façon certaine, peut-être à cause des techniques employées, de stades ultérieurs à l'anaphase hétérotypique. Néanmoins, il n'y a jamais de spermatides implantées dans des cellules nourricières, donc jamais de spermiogénèse dans des testicules morphologiquement normaux d'intersexués.

Parmi les figures de dégénérescence, on peut distinguer deux autres types:

—plaques très éosinophiles provenant de groupes de quelques cellules qui perdent leur structure interne, puis dégénèrent.

—trame cytoplasmique, sans trace de noyaux, qui délimite des espaces optiquement vides et occupe essentiellement la region distale du testicule.

Structure des Gonades de la Categorie 2 (Appareil mâle incomplet)

Dans tous les cas étudiés, elle s'est révélèe absolument identique à celle du testicule morphologiquement normal. On retrouve la même évolution des cellules germinales, les memes types et dispositions des figures de dégénerescence.

Conclusions

1. Toutes les glandes jaunes sont bien des testicules. Mais les observations que j'ai faites ne sont pas superposables à celles de Dobzhansky and Bridges (2). Au moins dans la souche que j'utilise, la structure cytologique est indépendante de l'évolution morphologique du testicule. Celui-ci possède les mêmes potentialités de croissance asymétrique que le testicule de mâle (3), mais son évolution cytologique est bloquée le plus souvent au stade diacinèse.

2. Au moins dans le cas que j'ai envisagé, la réunion d'un testicule et d'un oviducte n'entraîne pas de dégénérescence particulière du testicule.

3. Enfin des coupes ont été effectuées dans divers types de testicules quelques heures après l'éclosion de l'imago intersexué. Elles montrent que la mâturation des gonies intersexuées se développant dans le sens mâle est déjà stoppée à l'éclosion.

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APTERYGOTE MORPHOLOGY AND THE ORIGIN OF INSECTS

EVOLUTION OF THE HEAD MUSCULATURE IN INSECTS

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The most dominant evolutionary tendency of the head musculature has been towards the reduction in number of muscles. About one hundred muscles have been known in Thysanura but in the larva of the cyclorraphous fly, *Eristalis*, the number has been reduced to fifteen. This general tendency towards the reduction in number of muscles, however, has been resisted by six conservative evolutionary tendencies as follows:

1. A tendency for some muscles to become enlarged by proliferation of muscle cells and to split eventually into smaller independent muscles, e.g. an enormously developed posterior clypeo-epipharyngeal muscle in Psocoptera, which in the Mallophaga has evidently split into several independent muscles, associated with the change in feeding habits.

2. Some muscles remain unchanged while the structures, to which they are attached, have changed in their modes of development; e.g. the muscles of gnathal segments are attached to the tentorial supporting structure which is ectodermal in origin in the Thysanura-Pterygota, but in many other arthropods including the entognathous insects it is not of ectodermal origin. Yet many muscles attached to this internal skeleton are homologous.

3. Muscles moving their points of insertion and origin, accompanied by the displacement of the structures to which the muscles were originally attached. For example, as a result of rotation of the head and the displacement anteriorly of the ovoidal sclerite in Mallophaga, the muscles of the hypopharynx that are present in Psocoptera have come to be attached to quite different points of the hypopharynx.

4. The tendency for many muscles to change their points of insertion, accompanied by the reduction or loss of the structures upon which they were originally inserted. A salient example is the posterior frontal muscle of the labrum which has come to be inserted on the apodeme from the left mandible in Thysanoptera, accompanied by the loss of the left proximal angle of the labrum. This muscle has further become the protractor of the mandibular stylet in Hemiptera.

5. Muscles changing their points of origin while maintaining the original points of insertion. Strictly speaking practically all muscles have changed their points of origin during evolution whenever they encountered a new functional requirement. The loss of muscles has been prevented by this plasticity whenever such a new functional requirement of the organ with which they were associated was encountered. Sometimes newly acquired points of origin have persisted in some groups of insects. For instance, the tergo-galeal muscle, which has been known erroneously as the "tergo-palpal" muscle, has been derived from the stipito-galeal muscle. This tergo-galeal muscle is present in the larva of Mecoptera, Diptera, Trichoptera, and Lepidoptera.

6. The last conservative feature of the evolution of the head muscles is the tendency for some muscles to persist after the sclerotised structures, to which they were originally attached have become lost. For instance, the frontal protractors of the mouth-angle are inserted on the stomodaeal wall even after loss of the oral arm of the hypopharyngeal suspensorium.

THE MOUTHPARTS OF COLLEMBOLA

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Collembola may be grouped into four categories according to the form and function of their mouthparts, as follows: (1) biting and chewing; (2) rasping and sucking; (3) piercing and sucking; and (4) anomalous.

In the first type, the labrum is separated from the clypeus by a suture; each mandible has a well developed molar plate; the maxilla has a shoe-shaped cardo, a bipartite, boat-shaped stipes, a membranous maxillary palp, and a capitulum composed of outer, pointed lobes (galea) and inner, fringed lobes (lacinia). Two lateral plates constitute the labium and each plate is divided into three parts; submentum, mentum and labial palp. The hypopharynx consists of a single-lobed lingua and a bilobed superlingua bearing numerous fine teeth. The lingua is prolonged backwards into a pair of lingual stalks, each bearing three blunt lobes.

In rasping and sucking mouthparts, the clypeo-labral suture is indistinct or absent. Mandibles are not evident, or if present, lack molar plates. The maxilla is composed of a long, narrow cardo, an undivided stipes, and a capitulum comprising pointed lobes (galea) only. The hypopharynx is slightly modified or cup-shaped. The lingual stalk ends in a single, blunt lobe.

In piercing and sucking forms the mouthparts are concealed in a sclerotized buccal cone not found in the above two categories. A clypeo-labral suture may be present or not. The mandibles are similar to those of rasping and sucking forms. The maxilla is composed of a long, narrow cardo and a stipes, or of a stipes only. The hypopharynx has lingua and superlinguae well sclerotized and bilobed.

In the anomalous type, the mandibles are slender and elongate, without a molar plate. The maxilla has a long, narrow cardo, a stipes consisting of a single shaft, and a capitulum composed of outer (galeal) lobes and inner (lacinial) lamellae. The hypopharynx resembles that of piercing and sucking forms.

The mouthparts of Collembola have been compared with those of Diplura. There is little similarity between the two groups rearranged [1]. It is suggested that the systematic sequence conventionally used for the Collembola might be reversed, since the mouthparts of "Poduromorpha" (at least of those studied) appear to be the more specialized [2].

The functioning of the mouthparts has been observed in living *Isotoma olivacea* and *Neanura muscorum.* In the former, food particles are grasped by first protruding the maxillary palpi and then both mandibles. The galeae and laciniae scoop the food particles into the hypopharyngeal region where they meet the grinding surfaces of the mandibles. In *Neanura,* the pointed buccal cone first punctures the soft tissue. Mandibles and maxillae are then protruded which, tearing and piercing the tissue, presumably make the fluid material within accessible to the long, heavily sclerotized lobes of the sucking hypopharynx.

Our observations agree in general with the recent work of H. Wolter (1963, Zool. Jb. (Anat.) 81: 27-100).

1. Since this was written, Manton (1964, Phil. Trans. R. Soc. (B) 247: 1-183) has published a major work on mandibular mechanisms which is in agreement.
2. Since writing, Salmon (1964, Bull. R. Soc. N.Z., 7: 99-144) has published a new classification in agreement with this view.

LES SUPERLANGUES DES INSECTES INFERIEURS

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Les superlangues, bien développées chez quelques Insectes inférieurs seulement, ont pour équivalent les paragnathes des Crustacés. Ces structures postorales présentent un intérêt théorique, trop souvent négligé, dans la constitution de la tête des Insectes.

A la saillie hypopharygienne (langue et superlangues) se rattache une partie du plancher de la cavité préorale, allant jusqu'à la bouche. Cette partie reçoit typiquement l'insertion d'une paire de muscles (dilatateurs ventraux du cibarium), séparés des dilatateurs ventraux du pharynx par la commissure tritocérébrale (ou sa composante dorsale quand elle est double: Thysanoures).

L'innervation sensorielle de l'hypopharynx, connue en détail chez les Machilides est particulièrement intéressante:

(1) la lingua est desservie par une paire de nerfs, ayant chacun une double racine, mandibulaire et maxillaire;

(2) chaque superlangue est pourvue d'un nerf particulier, sortant du début de la masse sous-oesophagienne, au contact d'un nerf mandibulaire mais médialement à lui. Le nerf superlingual dessert également l'épiderme épaissi (pourvu d'épines exocuticulaires) de la base de la cavité cibariale. De plus la base de la superlangue reçoit un rameau issu du ganglion lingual;

(3) le domaine hypopharyngien dorsal, juste au-dessous de la bouche, montre un petit organe sensoriel pair, desservi par un court nerf venant du tritocerebrum.

La position des ébauches superlinguales chez l'embryon, médialement aux lignes joignant les lobes des futurs appendices gnathaux, et l'absence probable de cavités coelomiques sous-jacentes, tendent à faire considérer les superlangues comme de simples differenciations sternales du segment mandibulaire, secondairement unies à la lingua, saillie plurisegmentaire (au moins mandibulo-maxillaire).

Toutefois il n'est pas interdit de penser que les superlangues représentent les vestiges d'appendices d'un segment prémandibulaire régressé (et différent du tritocephalique). Leur constance chez de nombreux Arthropodes primitifs, leur nature paire et leur forme, leur innervation propre, au moins chez les Machilides, plaident en faveur de cette conception. Enfin si l'on rapproche ces formations du métastome des Trilobites, on est conduit à les considerer comme phylogénétiquement très anciennes: ce seraient les restes d'une lèvre inférieure primitive, équivalent ventral du clypéo-labre.

THE ENDOCRINE SYSTEM OF THE LEPISMATID THYSANURA AND ITS PHYLOGENETIC IMPLICATIONS

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In the Thysanura for which information is available (Machilidae, Lepismatinae and Atelurinae), the endocrine system includes all the major centres found in pterygote insects—medial and lateral neurosecretory cells, neurohaemal and glandular corpora cardiaca, corpora allata and ventral glands (1 and unpublished).

The medial frontal organ of the Lepismatinae has also been considered glandular (1). Electron microscopical investigations, however, have shown that it is a photoreceptor; the "discs" that join its groups of neurones are composed of hexagonal microvilli, as is the ocellar rhabdom of the lepidotrichid *Tricholepidion*, and the cytoplasm lacks elementary neurosecretory granules and contains little rough ER (2 and unpublished).

The medial neurosecretory cells of Machilidae, Lepismatinae and Atelurinae lie in the *pars intercerebralis* or in lateral frontal organs above the brain (1); the latter position is probably apomorphic. The neurosecretory cells show typical staining reactions, their axons form the *nervi corporis cardiaci* I and they contain elementary neurosecretory granules. Lateral frontal organs are necessary for the initiation of moulting in the lepismatid *Thermobia* (3), but not in the machilid *Petrobius* (4); and those of *Thermobia* are also involved in the metabolic changes associated with yolk deposition (unpublished).

The lateral neurosecretory cells are less well known, but neurones giving rise to *nervi corporis cardiaci* II occur in all groups (1 and unpublished).

The *corpora cardiaca* consist of discrete neurohaemal and glandular regions; the latter originates from the stomodaeum and is much reduced in machilids (1 and unpublished). The *corpora cardiaca* of Lepismatinae and Atelurinae therefore resemble structurally those of primitive pterygotes, but their physiology is unknown.

Thysanuran *corpora allata* are capsulate, vesicular glands lying in the base of the maxilla, and are innervated from the suboesophageal ganglion and the *corpora cardiaca* (1 and unpublished). As in pterygotes, they originate as ectodermal ingrowths between the mandible and the maxilla (5). The *corpora allata* of larval and adult Lepismatinae show juvenilising activity when implanted into saturniid pupae (5 and unpublished), and they appear to control scale development at the third larval moult (6 and unpublished; 7). Furthermore, yolk deposition in mated female *Thermobia* is correlated with active *corpora allata;* indeed, gonad stimulation is probably the primitive function of the gland.

Alleged ventral glands lie in the base of the labium in machilids, lepismatines and possibly atelurines. As neither embryological nor physiological data are available, their identification depends on their location and structure, and on their histological changes (1 and unpublished). In *Thermobia* the glands attain maximal volume at or just after the "critical period" for the brain hormone (3), and just before that for head ligature (Rohdendorf, *in litt.*), when the epidermis is synthesising DNA and its RNA content starts to increase (3 and unpublished).

Thus the Thysanura possess endocrine systems having the same plan as those of pterygotes, but presenting both plesiomorphic and apomorphic features. The large glandular *corpora cardiaca* of Lepismatinae and Atelurinae, and the role of the medial neurosecretory cells in moulting, suggest that the Lepismatoidea lie closer to the pterygote stem; but both subfamilies show specialization in the medial and lateral frontal organs. Studies of the relict *Tricholepidion*, of *Nicoletia* and of dipluran physiology could clarify these relationships.

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The unpublished data will appear in full elsewhere.

L'ENDOSQUELETTE THORACIQUE D'UN JAPYGIDE

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Récemment F. Carpentier et moi (1) avons publié un mémoire sur l'exosquelette thoracique des Japygides. Nous signalions (p. 101) qu'en plus des trois spinas l'endosquelette comportait une charpente sous-hypodermique. Celle-ci se compose d'une région médiane impaire (A) et d'un complexe latéral (B).

A. La portion médiane enveloppe la spina cuticulaire (fig. 2) et, en avant de celle-ci, elle se prolonge en une crête verticale débutant en avant du point de coalescence des deux branches de l'Y sternal (fig. 1). Cette portion rappelle la lame verticale médiane de *Campodea* (2). La gaîne spinale est raccordée au bord postérieur de l'intersternite (*is*) par les deux petites attaches endosquelettiques *1* présentes chez les autres Aptérygotes antérieurement étudiés. Ceux-ci, sauf les Collemboles (3) possèdent une tigelle squelettique reliant la portion spinale de l'endosquelette à la région intersegmentaire du flanc [voir *n* chez: *Campodea* (2), Lépismatides (4, 5, 6), Machilides (4)]. Chez le Japygide [comme chez le Collembole *Tetrodontophora* (3)], un muscle (fig. 1, n° 2), présente les mêmes relations. Les deux autres muscles (ibid., n^{os} 1 et 3), insérés aussi sur l'endosquelette médian, me paraissent typiques des Japygides: je n'ai pas trouvé leurs équivalents chez les autres Aptérygotes. Le premier est particulièrement intéressant: au prothorax il agit sur le stigmate segmentaire postérieur (*stp*), le seul de ce type chez les Japygides (1, p. 115). Aux deux autres segments le stigmate manque mais le sclérite "stigmatifère" (*x*) et le muscle persistent: un cas analogue a déjà été signalé (2).

B. Le complexe latéral, qui peut être qualifié de "furcal", est totalement sous-hypodermique. Sa partie principale (fig. 1, *f*) est une lame verticale naissant de l'hypoderme sur la branche latérale de l'Y sternal. Une très étroite tigelle (f') difficile à repérer, la relie à l'arc catapleural rétréci entre le sternum et la coxa; nous l'avions notée *f* dans le précédent travail (1) du fait que chez les autres Aptérygotes nous avions trouvé, assez fréquemment, une relation étroite entre l'arc catapleural et l'équivalent d'une furca de Ptérygote. La tigelle f' pourrait être un ancien muscle catapleuro-furcal ou coxo-furcal: on en voit de semblables chez les Chilopodes (7, 8).

Une bride anapleurale postérieure (*d*) relie la "furca" à la région du flanc où se touchent l'arrière de la pleure, la région postnotale (*pt*) et l'extrémité latérale du sternum, comme cela existe chez d'autres Aptérygotes. Chez le Japygide comme chez *Lepisma* (4) elle sert à l'insertion de muscles longitudinaux ventraux.

Une tige assez robuste (b'') relie la "furca "à la crête médiane; elle ne supporte aucun muscle. Je l'assimile à l'une des tigelles mésothoraciques de *Petrobius* (3)† ou à une tigelle prothoracique de *Nicoletia* (6).

Une bandelette extrêmement grêle (b') repérée au seul prothorax, relie la base de la furca à l'extrémité antérieure de la crête médiane. Je la rapproche d'une tigelle mésothoracique de *Petrobius* (3)† et du prothorax de *Lepismachilis* (inédit).

Dans son ensemble l'endosternite du Japygide est plus simple que celui des autres Aptérygotes. Plusieurs attaches, présentes même chez *Campodea* (2), manquent ici, telle l'importante tigelle pleurale *p*. Ce qui subsiste du complexe furcal rappelle davantage les Thysanoures. Chez le Japygide les parties médiane et latérale de l'endosternite restent mieux individualisées qu'elles ne le sont chez les autres Aptérygotes déjà étudiés.

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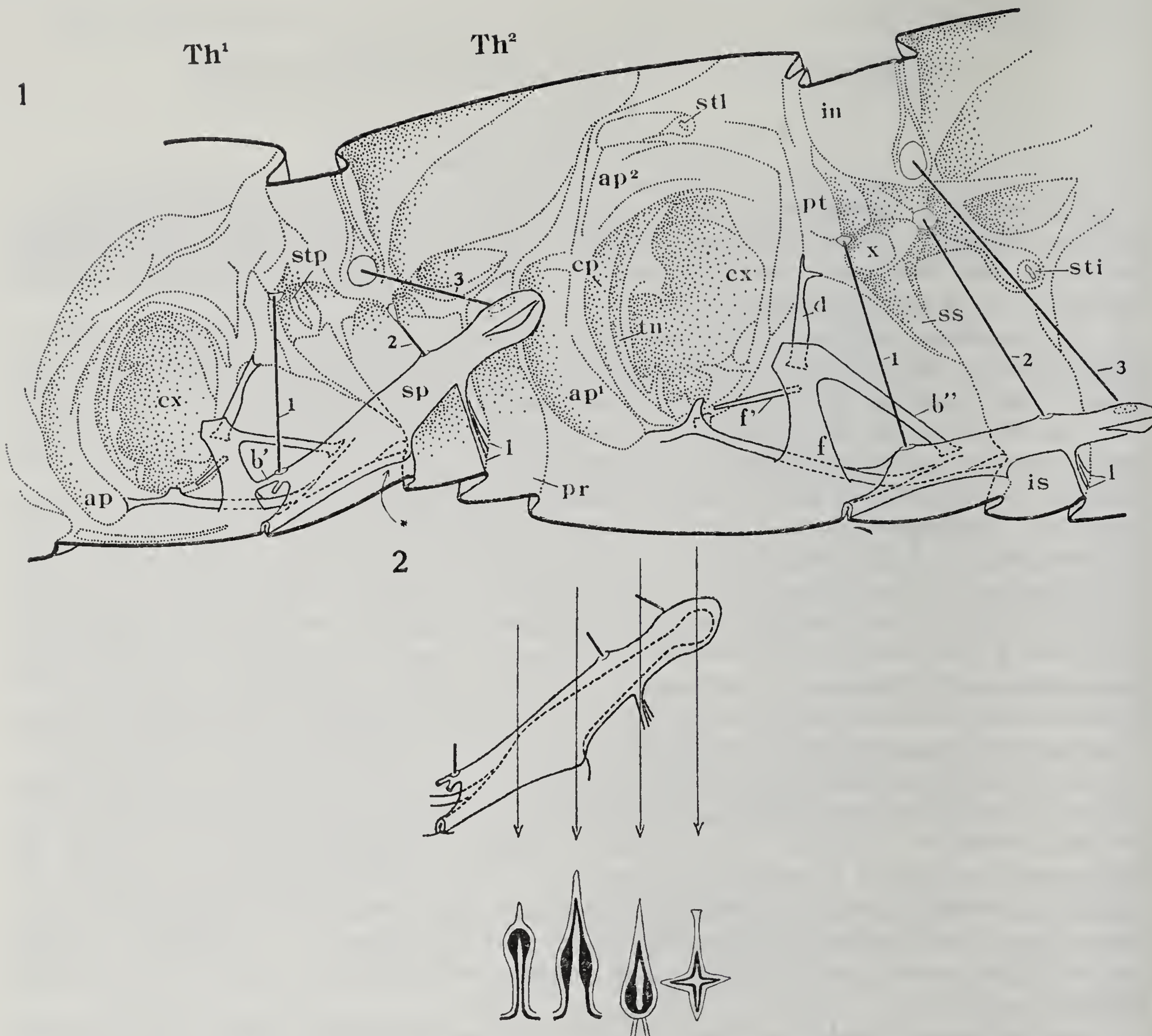
†Sans notation sur la fig. 1 de ce travail.



Figs. 1-2. (1) Moitié droite du squelette de la région sterno-pleurale des pro- et mésothorax d'*Oncojapyx basilewskyi* Pagès, vu par l'intérieur; (2) Vue latérale transversales, à quatre niveaux successifs, de la spina pιothoracique.

Abreviations:

Les abréviations figurant au mésothorax n'ont pas été toutes reprises au prothorax.
Th_1, Th_2: prothorax, mésothorax; ap: anapleure ou arc anapleural; ap_1: anapleurite proximal ou "mérosternite"; ap_2: anapleurite distal; b': bride endosternale prothoracique; b'': tigelle endosternale; cp: arc catapleural; cx: coxa; d: bride anapleurale postérieure; f: lame sous-hypodermique tenant lieu d'apophyse furcale; f': tigelle furco-catapleurale; in: internotum; is: intersternite; l: attaches spinales postérieures; pr: présternite; pt: région postnotale; sp: spina; ss: spinisternite; sti: stigmate intersegmentaire; stl: stigmate suprapleural; stp: stigmate postsegmentaire (prothoracique); tn: trochantin; x: sclérite homologue au sclérite stigmatifère prothoracique.

*: entrée de la cavité de la spina cuticulaire, lieu homologue à l'attache spinale antérieure *a* des autres Aptérgotes. 1: premier muscle endosterno-pleural (stigmatique au prothorax); 2: second id., homologue à la tigelle *n* des autres Aptérygotes; 3: muscle spinto(inter)notal.

MORPHOGENESIS AND REGENERATION

MORPHOGENESIS OF LOCUST CUTICLE

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(*i*). Adult locusts produce both rubber-like cuticle and ordinary solid cuticle. The rubber-like cuticle occurs in elastic energy-storing pads at the wing base (8), and contains the rubber-like protein resilin. Convenient samples of both kinds of cuticle occur in locusts.

(*ii*). Locust cuticle is transparent and is not obscured by pigmentation or sclerotization, making possible birefringence analysis.

(*iii*). Locusts deposit both kinds of cuticle in daily increments, giving rise to daily growth layers whose morphogenesis can be altered by varying rearing conditions at the time of deposition (5, 6, 7).

Daily growth zones in resilin can be seen in ultra-violet light when they appear as wide brightly fluorescent zones (day zones) alternating with thin faintly fluorescent zones (night zones). The fluorescence is due to two new amino acid derivatives of tyrosine, built into the polypeptide chains and covalently cross-linking them into a three-dimensional molecular network (1). In contrast to solid cuticle resilin is cross-linked in parallel with its deposition (6). Thus the variation in fluorescence between resilin deposited in day or night conditions may reflect variations in the degree of cross-linking within the molecular network. Resilin deposited in constant day conditions, (light, 38°C), is brightly fluorescent and lacking in zonation.

The daily growth zones in solid cuticle consist of night layers each of several chitin lamellae alternating with non-lamellate day layers. Chitin lamellogenesis can be inhibited in cuticle grown in constant day conditions, providing non-lamellate samples which can then be compared with lamellate samples. With 30 minutes night allowed in the middle of a week of otherwise constant day conditions, a single chitin lamella is organised.

Birefringence analysis shows that the chitin framework of solid cuticle contains three components: (*a*) chitin lamellae, with the chitin crystallites oriented parallel to the plane of the cuticle surface, (*b*) pore canal fibrils, running radially through the cuticle, (*c*) longitudinal fibrils running along the leg or wing vein axis. Of these, chitin lamellae can be inhibited by constant day conditions during deposition. Longitudinal fibrils are also morphogenetically alterable by growing pieces of leg as transplants in the haemocoel.

In constant night, (dark, 38°C), the daily deposition rhythm persists for at least two weeks and is thus circadian. Thus morphogenesis in locust cuticle is linked to a biological clock. Interaction between biological clocks and environmental factors may influence insect morphogenesis over both long and short term periods and at various levels of structure. Thus termination of diapause and onset of pupation in cornborer larvae (2), polymorphic differentiation in aphids (4) and tumour formation in cockroaches (3) are all examples of circadially influenced morphogenesis at the tissue level. Changes at the ultrastructural level (organisation of chitin crystallites) or perhaps at the molecular level (resilin cross-linking) may also be circadially organised, possibly via similar endocrine pathways.

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THE FORMATION OF INSECT CONNECTIVE TISSUES

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The structure of insect connective tissue has been investigated extensively, but nothing was known of its formation, though it had been suggested that both the haemocytes and the cells underlying the tissue were implicated in its production. In a recent study of the development of the adult connective tissue associated with the CNS of *Galleria mellonella*, it was shown that the sheath cells only are responsible for the formation of the adult neural lamella and the extra mass of connective tissue on the dorsal side of the abdominal region of the nervous system, which is peculiar to the Lepidoptera (2).

An electron microscope study of this developing tissue in *Galleria* (1) revealed striking similarities between the sheath cells, or fibroblasts, of the moth and those of the vertebrates. The most conspicuous cytoplasmic inclusions are a series of vesicles enclosing a substance more electron dense than the surrounding cytoplasm. The membranes surrounding these vesicles can, in some instances, be seen to be continuous with the membranes of the cisternae of the granular endoplasmic reticulum and with the outer nuclear membrane, and thus they are identified as dilatations of the endoplasmic reticulum. A similar form of dilated endoplasmic reticulum is commonly found in vertebrate fibroblasts. It is considered that the collagen molecules are synthesised by the ribosomes on the cisternae of the endoplasmic reticulum and then passed into the lumen of the cisternal and vesicular system.

Intracellular fibrils are frequently seen in moth fibroblasts; they appear to be hollow and in some places banding with a periodicity between 12 and 20 mμ may be seen. It is thought that these fibrils and their surrounding cytoplasm become incorporated into the fibrous connective tissue. In the dorsal mass of connective tissue, no intracellular spaces are formed, and the increase in area of the fibrous tissue is at the expense of the cytoplasm of the cells. Where the cytoplasm of a cell and an area of fibrous tissue are adjacent, the plasma membrane of the cells cannot be distinguished and so it is suggested that there may be an actual syncytium with the fibrous tissue existing in the syncytial cytoplasm.

The fibrous tissue in the moth is unusual as the fibrils are obscured by masses of a ground substance thought to be acid and neutral mucopolysaccharides; the fibrous areas give a strongly positive PAS reaction and stain metachromatically with toluidine blue (3). In a few places, the fibrils are incompletely covered and there are indications that these fibrils are identical with the intracellular fibrils. Thus it seems that the fibrils are formed intracellularly and then, as they become incorporated into the fibrous tissue, the ground substances surround and obscure them.

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OBSERVATIONS ON THE METAMORPHOSIS OF THE NERVOUS SYSTEM IN THE FLY *SARCOPHAGA* AND OTHER DIPTERA CYCLORRHAPHA

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In the cyclorrhaphan larva the ganglia are concentrated into an anterior nerve mass. Paired lateral segmental nerves pass to their respective segments, and a branch of the eighth abdominal nerve passes along the hind gut. A series of seven mid-dorsal nerves also arise and diverge into left and right branches, passing into the musculature of abdominal segments two to eight. These almost certainly correspond to the visceral nerves of other insects. Three pairs of thoracic and seven pairs of abdominal tracheae tracheate their respective ganglia.

In the adult the appearance is very different from that of the larva. The thoracico-abdominal mass is separated from the sub-oesophageal ganglion and brain by a long cervical

connective. The abdominal centre is enormously reduced by comparison with the thoracic region and there is a highly complex arrangement of thoracic nerves. In contrast the abdomen is innervated by two fine paired and a single bifurcating median abdominal nerve in *Drosophila melanogaster* and *Phormia regina*, and by a single pair of lateral and the bifurcating median nerve in *Sarcophaga bullata*. In *Phormia* and *Sarcophaga* although the positions of origin of branches from the median nerve is variable and asymmetric, their segmental distribution is shown to be constant. Ventral tracheation is by three thoracic pairs of tracheae only.

In tracing the development of the system it has been found that the larval lateral nerves are not histolysed. In the pre-pupal stage, orcein preparations show cell division occurring among the sheath cells of these lateral nerves. There is an enormous increase in sheath cell number. By the second day of pupation the neural lamella over the nerves and that of the ventral nerve mass itself has disappeared. Once the outer restricting membrane is removed cell growth and proliferation can occur. New thoracic branches arise. Also an overall shortening of the abdominal lateral nerves seems to be brought about by retraction of individual sheath cells. This process, together with active growth at the posterior end of the nerve mass, brings about the formation of the median abdominal nerve; the bases of the lateral nerves are "carried" posteriorly in the growth process. When proliferation is completed, the adult nerve sheath is secreted, along with the basement membrane of associated tracheal elements.

The dorsal nerves are not carried over into the adult stage, and disappear at the same time as the neural lamella and the epithelium of the larval abdominal tracheae. Light and preliminary electron microscope evidence supports the suggestion that, in the pre-pupal stage, the lateral and dorsal nerves produce secretions which may influence differential tissue histolysis.

A comparable sequence of cell mitosis followed by disappearance of the sheath occurs in a string of cells passing from the larval gonad to the ventral musculature. After breakdown of the sheath there is a shortening of the cord and a thickening to form a tube which certainly contributes to the gonadial ducts. This string of cells represents what would therefore appear to be a new "imaginal rudiment".

VORGÄNGE BEI DER INNEREN METAMORPHOSE DES KOPFES VON *OSMYLUS CHRYSOPS* L. (NEUROPTERA, PLANIPENNIA)*

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Die Larve von *Osmylus* ist prognath und hat hochspezialisierte Saugstilette. Die Imago ist orthognath und unspezialisiert. Die Umformungen während der Metamorphose werden meist mit den Prozessen der "Histolyse" und "Histogenese" charakterisiert. Aber ein Abbau ganzer Gewebe tritt nur sehr vereinzelt auf. Meist werden nur die Differenzierungsprodukte der einzelnen Gewebe in der praepupalen Phase partiell, selektiv und graduell verschieden stark entdifferenziert und verlagert. Nicht nur die Endocuticula wird beim Beginn der inneren Häutung von der Epidermis abgelöst und kurz vor der Verpuppung aufgelöst, sondern auch die sklerotisierten Schichten der larvalen Cuticula werden umgebaut. Das zeigt sich besonders in der Mesocuticula, d.h. in den inneren Partien der "Exocuticula", die einen anderen chemischen Aufbau und daher eine spezifische Anfärbbarkeit besitzen. Diese Schichten nehmen z.T. bei dieser Entsklerotisierung wieder endocuticularen Charakter an, wodurch die Endocuticula voluminöser wird. Das zeigt, dass der Vorgang der Sklerotisierung z.T. reversibel ist. Dieser Prozess erfasst bei den Teilen mit schwacher oder fehlender Exocuticula—z.B. and er Häutungsnaht, dem Occiput und dem ganzen Endoskelett—die gesamte Mesocuticula. Lange vor dem allgemeinen Abbau der Endocuticula wird selektiv an der hier mächtigen Postoccipitalleiste und an Teilen der vorderen Tentoriumarme auch noch die ganze Endocuticula abgebaut, sodass das praepupale Endoskelett fast nur mehr aus Epidermis besteht.

* Mit Unterstützung der DEUTSCHEN FORSCHUNGSGEMEINSCHAFT. Diese Arbeit wird in ausführlicher Form in den Zoologischen Jahrbüchern Abt. Anatomie erscheinen.

Diese Entsklerotisierung ermöglicht die Verlagerung des Kopfmaterials in den Halsteil der Larve, sowie später das Aufspringen der Kopfkapsel an der Rissnaht. Die Verlagerung ermöglicht den Umbau. Durch entsprechende Kontraktion der Halsmuskulatur wird der ganze Larvenkopf nach ventral gezogen (Abb. 1). Dabei wird das innere Kopfmaterial ungleichmässig aus seinen cuticularen Hüllen gezogen und daher gleichzeitig mit dem Herausziehen umgeformt. Dies führt z.B. im labro-epipharyngealen Bereich zu einer Umrollung epipharyngealer Partien auf die dorsale Kopffläche. Der bei der Larve mit dem unabgegliederten Labrum nur durch seine Innervierung zu identifizierende Musculus frontolabralis (M1) kommt dabei in seine typische Lage. Diese Ausrollung des Vorderkopfes bei der Metamorphose dürfte ein Hinweis darauf sein, dass in der Embryonalentwicklung diese Spezialisation der nur lateral offenen Praeoralhöhle wohl durch eine Einrollung der vorderen Kopfpartien zustande gekommen ist.

Die Formen werden also durch Zellverschiebung verändert und erst danach durch Wachstum vergrössert. Gleichermassen vollzieht sich die Umprägung des Endoskeletts und der spezialisierten Mundwerkzeuge zu den orthopteroid gebauten Teilen der Puppe.

Parallel mit diesen Prozessen an der Larvencuticula geht die Entdifferenzierung an der Muskulatur ebenso partiell, selektiv und zeitlich verschieden. Sie führt nicht zum völligen Abbau ganzer Muskeln. Dicht beieinander liegende Muskelbündel können einen ganz verschiedenen Entdifferenzierungsgrad aufweisen. Aber kein Muskel wird unverändert in die Imago übernommen. Die meisten pupalen Muskel sind auf Larvalmuskeln zurückzuführen, die gegebenenfalls verkürzt oder vergrössert und verlagert wurden.

Nicht die Muskelursprünge wandern und sind damit unzuverlässige Zeugen der Skelettteile, sondern die Kopfbezirke, welche die Skeletteile aufbauen, verschieben sich in ihrer Form und Lage.

Was bei der äusseren Metamorphose als ein grundlegender Neubau einer Organisation erscheint, ist im Inneren nur eine Umlagerung wachsender Teile. Dabei ist der charakteristische Prozess—zumindest bei diesem relativ ursprünglichen Holometabolentyp—nicht die Histolyse, sondern die partielle Entdifferenzierung. Durch diesen Prozess lösen sich die Bauelemente in der praepupalen Phase von ihren adaptiven Strukturen und formen sich um zum imaginalen Bautyp. Die Organisation dieses Larvenkopfes ist daher nur eine Form einer Mehrzweck-Konstruktion.

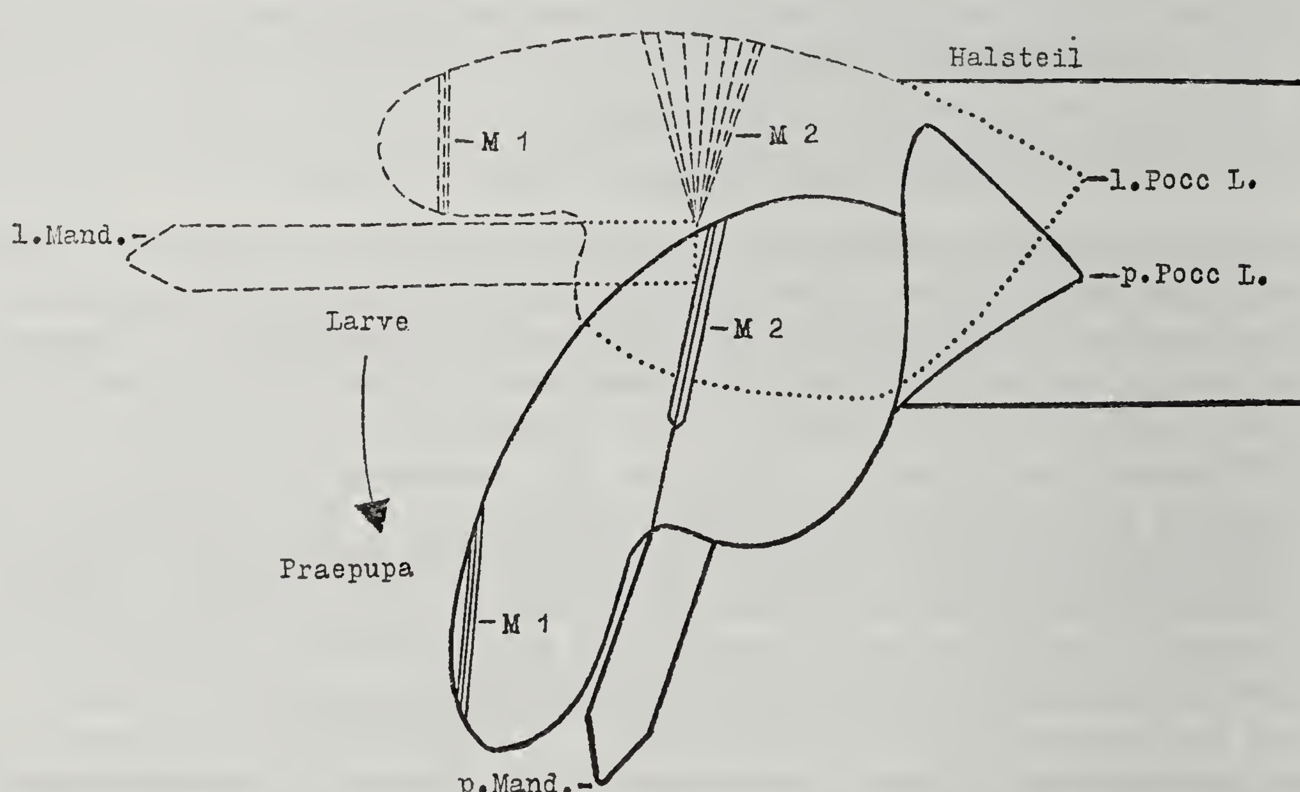

Abb. 1. Schematisierte Lateralansicht der Kopfkapsel und des Halsteils von *Osmylus*. Von den Mundwerkzeugen nur die Mandibel eingetragen. Unterbrochene Linie: Kopfstellung der Larve; ausgezogene Linie: Kopfstellung in der praepupalen Phase; M 1: Frontolabralmuskel; M 2: Teil des Mandibel-Abduktors; l. Mand.: larvale Mandibel; p. Mand.: pupale Mandibel; PoccL: Postoccipitalleiste, deren epidermaler caudaler Anteil sich in der praepupalen Phase von dem cranialen Anteil zur Umformung abgehoben hat.

SKELETO-MUSCULAR MORPHOGENESIS IN THE THORAX OF THE HYMENOPTERA

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During transformation of the skeletomuscular system of the larval mesosoma of the honey bee into that of the imago, all larval muscles are destroyed, but most of the bands are associated with the development of pupal muscles. However, the majority of the pupal muscles are formed by groups of myblasts which are independent of the larval bands. Twelve of the muscles in the pupa degenerate before the adult stage is reached. It is believed that these pupal muscles function during metamorphosis before they degenerate, but their specific effects remain to be elucidated. Various other muscles are believed to have effects on the genesis of the imaginal skeleton. Certain apodemes are clearly associated with muscles. The parapsidal lines, anteroadmedian lines, and subpleural signa are the sites of the attachments of the rudimentary indirect flight muscles. The notauli, median line, and transpropodeal lines appear to be associated with the distribution of connective tissues. Many other features of the pupal and imaginal skeletons, however, develop without connection to internal tissues.

Turning now to a comparison of the anatomy of the honey bee with other Hymenoptera, dissections of female adults of *Xyela minor* Norton and male adults of *Sirex behrensii* (Cresson) reveal that each of the twelve strictly pupal muscles of *Apis* can be homologised to adult muscles in one or the other species of primitive Hymenoptera. It seems likely that the muscles persist in the honey bee because of definite roles in metamorphosis and not as a recapitulation of ancestral musculature.

With regard to features of the skeleton, the parapsidal lines, anteroadmedian lines, subpleural signa, notauli, and median mesoscutal line are frequently present on the mesothorax of hymenopterans. Knowledge of the developmental anatomy of these structures and their association with other tissues aids in recognition and homology. A comparative survey of adult representatives from each of the superorders of the Hymenoptera shows that the subpleural signa, anteroadmedian lines and parapsidal lines are present only in the Siricoidea among the Chalastogastra and in all superfamilies of the Clistogastra except the Chalcidoidea and most of the Ichneumonoidea. These marks are associated with the attachment of fibrillar muscles to the epidermis during metamorphosis. Many species of Hymenoptera have muscles of the fibrillar histological type other than the well-known dorsoventral and longitudinal flight muscles (1). It is not surprising, then, to discover additional marks on the integument in certain species with additional fibrillar muscles. The absence of all marks of this kind in most Chalastogastra, even though fibrillar muscles are present, must indicate a different kind of morphogenetic relationship between the muscles and the epidermis.

The notauli and median lines are associated with the distribution of connective tissues during metamorphosis. The nature of this relationship is not known, but the notauli trace externally the line of attachment of a pair of dorsal tracheal tubes and the median line traces the attachment of the medial dorsal septum of the aorta. In a comparative survey, these sulci are found in some species in each of the superfamilies of Chalastogastra and in varying degrees of expression in virtually all superfamilies of the Clistogastra. The notauli are the conspicuous furrows on the mesoscutum of many chalcidoids.

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THE ANALYSIS OF INSECT MORPHOGENESIS BY MULTIVARIATE STATISTICAL METHODS

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Most quantitative investigations of insect growth have been analyses of size, expressed by weight or by a very few linear dimensions, sometimes combined in some simple function. The more complex problems presented by changes of shape have received far less quantitative consideration, though the pioneer study of D'Arcy Thompson drew attention to them nearly fifty years ago. With the development of electronic computing facilities, methods which permit the statistical analysis of shape have now become practicable and a few such multivariate techniques have already been applied to the growth of vertebrates. Their use in the study of insect development has, however, been indirect and confined largely to differences of adult shape in polymorphic or geographically variable species. The recent analysis of postembryonic development in *Dysdercus fasciatus* Sign. (Pyrrhocoridae) by Blackith, Davies and Moy (*Growth*, 1963, 27: 317-334) seems to be the first direct application of multivariate techniques to insect growth and development.

The primary data consisted of replicated measurements of the median lengths of the head, thoracic and first seven abdominal segments, together with estimates of the breadth of the body at four points. Analysis of such data enables one to depict the developmental stages of the insects as points dispersed in a system of orthogonal axes corresponding, in this case, to three statistically independent patterns of growth.

The most important of these, accounting for some 65% of the total variability, involves effects on the insect's shape due to increasing size, i.e., it represents a generalised form of allometric growth, not only in the normal sense of this term, but also in the sense that the growth increments for each of the measured characters are not constant during development. The second growth pattern, absorbing about 22% of the total variability, involves characteristic changes associated with the development of male characteristics during the last preimaginal stadium, while the third growth pattern, making up about 11% of the total variability, is connected with comparable changes in the female.

Biologically, an interesting feature is the way in which all three growth patterns change abruptly at the transition from the last preimaginal instar to the adult. The trend previously operative in the first mode of growth is greatly accentuated at this time, while striking reversals occur in the second pattern—for males—and in the third for females. These abrupt transitions are hardly if at all apparent on inspection of the original measurements, but clearly correspond to the relatively great morphogenetic changes which constitute the hemimetabolous "metamorphosis" of the species. Methods such as this therefore seem to provide not only techniques for following the changing shapes of developing structures or of whole insects, but also offer promising ways of comparing quantitatively the intensity and time relations of metamorphosis in different taxonomic groups of hemimetabolous insects.

THE EMBRYOLOGY OF THE STOMODEAL NERVOUS SYSTEM IN *AULOCARA ELLIOTTI* THOMAS (ORTHOPTERA, ACRIDIDAE)*

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From a series of fixed, known-age embryos, criteria were formulated based on external morphological changes to divide the embryogenesis into twenty-seven developmental stages. Of these, eighteen represented the pre-diapause development, one was designated as the diapause stage, four concerned the revolution period, and four portrayed the post-revolution development including the definitive embryo. It was learned that most embryos reached the diapause near the fortieth day of age at 25°C.

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The subesophageal body is the first head gland to appear in the *Aulocara* embryo and it first was observed in Stage 9 embryos. This organ arises from paired regions of dorso-lateral hypoderm in the mandibular segment and additional cells appeared to be derived from those regions for several stages. Cytological changes were observed during the embryogenesis and prior to the definitive stage, the number of subesophageal body cells becomes greatly reduced.

The stomodeal ganglia appear in Stage 13 embryos as incrassations on the dorsal wall of the stomodeum. At a little later stage the first anlage could be identified as the frontal ganglion, the second as the common anlage of the occipital (hypocerebral) ganglion and the corpora cardiaca, the third as the source of the paired ingluvial ganglia. Differentiation of cell types in these ganglia was begun prior to the diapause stage and the sizes of these organs do not appear to change greatly after that stage.

A series of lateral hypodermal invaginations are formed beginning between the antennae and mandibles. The first pair form the anterior tentorial arms and near their bases smaller invaginations appear which are believed to be the anlagen of the corpora allata. As the rudimentary corpora allata migrate medially with the anterior tentorial arms, incrassations appear at the ventro-posterior margins of the adjacent antennary coelom. Similar mesodermal modifications were observed near the corpora cardiaca. Prior to the diapause stage, the corpora allata have reached their positions at the sides of the stomodeum. Paired invaginations between the mandibles and maxillae form the mandibular apophyses, and posterior to the bases of the maxillae, the posterior tentorial arms invaginate. The ventral head glands, (prothoracic glands) appear as small invaginations between the maxillae and the labial appendages near Stage 13. Because of the change in the position of the mouthparts later in the embryology, the intersegmental relationship of these organs becomes obscure. At about the 14th Stage, invaginations of the labial glands arise in that segment and at Stage 19, the common salivary duct is visible at the base of the hypopharynx.

As early as Stage 12, the migration of groups of ganglion cells from the ventral nerve cord into the gnathal appendages can be observed. The development of a pair of these peripheral ganglia in the labrum, mandibles, maxillae, and labium was observed and in the hypopharynx, a single ganglion with paired nerves was found.

DEGENERESCENCES PYCNOTIQUES AU COURS DU DEVELOPPEMENT DU TESTICULE CHEZ *GRYLLUS DOMESTICUS* L. (ORTHOPTERA)

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L'ébauche des gonades apparait chez l'embryon aprés la formation du mésoderme (cas des Hétérométaboles). Les cellules germinales sont localisées au niveau de la paroi interne des cavités coelomiques ; du deuxiéme au sixiéme segment abdominal chez *Gryllus domesticus L.* Le problème de l'origine des cellules germinales n'est pas encore défini avec certitude (Heymons 1895, Wheeler 1893, Roonwal 1937, Seidel 1924, Nelsen 1931.) En fin de blastocinése, le matériel méso dermique des gonades s'isole en deux bandelettes dorso-latérales contenant au niveau de chaque segment un groupe de quelques gonies.

Chez l'embryon de *Gryllus domesticus L.*, 10 jours aprés la ponte (incubation 25°, développement 21-22 jours) ces bandelettes sont identiques dans les deux sexes. Entre 11-12 jours, elles se rétractent, forment des replis, et l'ébauche des gonades n'occupe plus que les segments trois et quatre. Les gonies sont alors groupées en une seule masse, ventralement à la bandelette, au niveau du troisiéme segment. A cet àge débute chez le mâle une crise de dégénérescences nucléaires (colorations: Feulgen, Mann-Dominici). Les lobes des replis deviennent peu nets et le tissu mésodermique montre toutes les étapes de la pycnose: (Trowell 1952)

—chromatine condensée en amas de dimensions variables
—chromatine à la périphérie du noyau, au centre une vacuole
—chromatine condensée en une sphère dense
—la sphère se fragmente en sphérules de tailles variables.

Entre 13-14 jours, les spermatogonies sont englobées à l'intérieur de ce tissu, le nombre de noyaux en dégénérescence est maximum et le testicule est de forme ovoïde. 16 jours aprés la ponte, la crise de pycnose se termine, le testicule est devenu sphérique, il va garder cet aspect jusqu'à l'éclosion et pendant le premier stade larvaire.

Chez la femelle (10-11 jours aprés la ponte) les replis de la bandelette restent nets, ils se tassent dans la région antérieure de la gonade. On n'observe pas de noyaux en dégénérescence pycnotique. 13-14 jours aprés la ponte, les replis s'organisent autour d'une courte portion antérieure de la bandelette, portion se poursuivant par le filament terminal et où se produisent, à cet âge, quelques pycnoses, seules dégénérescences observées au cours de l'organogenèse de l'ovaire. Les ovogonies occupent la région médiane de l'ovaire.

Au deuxiéme stade larvaire se produit dans le testicule une nouvelle crise de dégénérescences nucléaires. Les noyaux en pycnoses sont abondants dans la région des spermatogonies; les sphérules, étape ultime de la dégénérescence, se rassemblent dans la zone centrale du testicule. Ces particules sont Feulgen-négatives, contrairement aux noyaux à l'état de sphères ou d'amas. Ces pycnoses portent probablement à la fois sur les spermatogonies et le matériel mésodermique. L'ensemble parait bloqué dans son développement jusqu'au quatrième stade larvaire, où débute la formation des cystes et les mitoses goniales.

DIMORPHIC RESPONSES OF TRANSPLANTED GONADAL ANLAGEN OF MOSQUITOES

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Dimorphism of *Aedes stimulans* is under environmental control during larval development (1, 2). Genotypic male larvae develop into imaginal males only if the rearing temperature is low. Phenotypic females are produced when larvae bearing the male genotype are exposed to abnormally high but sublethal temperatures. To determine which organs temperature affects directly, plastic gonadal discs of *A. stimulans* were transplanted into larvae which were reared at given temperatures.

Initially, the gonadal discs of genotypic male larvae have the capability of developing into either ovaries or testes. Gonadal discs retain their plasticity during instars 1 and 2 when the rearing temperature is 27°C. If larvae are subsequently reared at 18° for instars 3 and 4, the gonads are testes, whereas ovaries develop if the rearing temperature is 27°.

Gonadal discs were extirpated from larvae at the beginning of instar 3, and they were implanted into receptor larvae of the same age which were reared at either 27° or 18° for instars 3 and 4.

To determine if the factors controlling differentiation of a plastic disc into the male form are inherent in the imaginal discs or if they are humoral in nature, each of the two gonadal discs of an *A. stimulans* donor was implanted into a separate receptor which was subsequently reared at 18° for instars 3 and 4. Implanted gonads developed into testes in both male and female receptors. Thus, factors responsible for the differentiation of a plastic organ into the male form are inherent in the imaginal discs. If sex hormones had been responsible for differentiation, then the disc placed into a female receptor should have developed into an ovary.

The second experiment was designed to demonstrate the plasticity of the gonadal discs and to amplify the results of the first one. Each of the two gonadal discs of an *A. stimulans* donor was implanted into separate receptors of the same species. one reared at 27° and the other at 18° for instars 3 and 4. That reared at 27° developed into an ovary, the other into a testis (table 1). The organs which temperature is affecting directly are not indicated. A temperature of 27° during all four instars wholly feminizes the receptor gonads as well as those of the donor (table 1). Since the receptor gonads are ovaries at 27°, it is not possible to ascertain if the implanted disc underwent differentiation into an ovary independently of factors in the hemocoel.

To determine if differentiation of a plastic gonadal disc into an ovary is controlled by factors extrinsic to or intrinsic in the imaginal discs, it was necessary to use receptors, such as larvae of *A. vexans*, which are masculinized at 27°. Plastic gonadal discs of *A. stimulans* implanted into male receptors of *A. vexans* which were reared at 27° for instars 3 and 4 developed into ovaries (table 2). Thus, differentiation of a plastic organ into the feminine form is due to factors intrinsic in the imaginal discs. If sexual hormones had been responsible for differentiation, then the disc placed into a male receptor should have developed into a testis.

Temperature controls dimorphism of *Aedes stimulans* through factors intrinsic in the imaginal discs. Gonadal discs undergo differentiation into testes or ovaries in response to temperature alone and not in response to the humoral environment surrounding the developing organ. Sexual hormones do not control dimorphism in this species of insect.

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Table 1

Imaginal differentiation of the two gonadal discs of each donor of *Aedes stimulans* transplanted into separate receptor larvae of the same species, one of which was subsequently reared at 27° and the other at 18° for instars 3 and 4.

Genotype for dimorphism of donor	*Designation of each gonadal disc of donor*	*Genotype for dimorphism of each receptor*	*Rearing temperature of each receptor during instars 3 & 4*	Phenotype of imaginal gonads *Receptor*	*Donor*
Male	a	Male	27°	ovaries	ovary
	b	Male	18°	testes	testis
Male	a	Female	27°	ovaries	ovary
	b	Female	18°	ovaries	testis
Male	a	Female	27°	ovaries	ovary
	b	Male	18°	testes	testis
Male	a	Male	27°	ovaries	ovary
	b	Female	18°	ovaries	testis

Table 2

Imaginal differentiation of the two gonadal discs of each donor of *Aedes stimulans* transplanted into separate receptor larvae of *Aedes vexans*, one of which was subsequently reared at 27° and the other at 18° for instars 3 and 4

Genotype for dimorphism of donor	*Designation of each gonadal disc of donor*	*Genotype for dimorphism of each receptor*	*Rearing temperature of each receptor during instars 3 & 4*	Phenotype of imaginal gonads *Receptor*	*Donor*
Male	a	Male	27°	testes	ovary
	b	Male	18°	testes	testis
Male	a	Female	27°	ovaries	ovary
	b	Female	18°	ovaries	testis
Male	a	Female	27°	ovaries	ovary
	b	Male	18°	testes	testis
Male	a	Male	27°	testes	ovary
	b	Female	18°	ovaries	testis

SUR LA TRANSPLANTATION D'APPENDICES CHEZ LA BLATTE *BLABERUS CRANIIFER* Burm.

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Au cours d'une étude sur la régénération des appendices de *Blaberus craniifer* Burm., nous avons pratiqué des greffes de pattes en différents territoires. Nous avons procédé en deux temps:

—Transplantation d'appendices en territoires qui ne comportent pas normalement d'appendices (tergites, sternites).

—Transplantation d'appendices en territoires qui comportent normalement un appendice différent (patte à la place d'autres pattes, patte à la place d'antenne).

Nous avons pu remarquer que la réussite de la greffe dépend à la fois du greffon et du porte-greffe. Si le greffon est transplanté en territoire ne portant pas d'appendice normalement, il garde sa spécificité primitive et il régénère en ce sens. La patte ne semble nullement subir l'influence de sa nouvelle situation. Les régénérats sont différents si la transplantation se fait en territoire portant normalement un autre appendice. Il y a dans ce cas compétition entre les deux territoires. Il y a régulation plus ou moins rapide, le territoire porte-greffe tend à dominer.

Dans tous les cas, nous nous heurtons au phénomène de croissance discontinue qui chez les Insectes rend également l'observation discontinue. Le greffon pourrait peut-être prendre avec ses caractères propres, mais il doit subir une croissance et une prise à travers le phénomène de mue. S'il prend, ses caractères de greffon entrent en compétition avec les substances du territoire d'implantation.

L'animal se recompare continuellement à son schéma général, il y a retransformation partielle de l'individu à chaque période d'intermue, refonte d'une partie des tissus pendant laquelle le greffon perd de plus en plus ses caractères propres pour être impressionné par les caractères de la région ou il se trouve.

Ceci s'oppose à ce qui a pu être observé chez les animaux à croissance continue; en effet, dans ce cas, une fois terminée la période embryonnaire, l'animal subit une croissance lente sans dédifférenciation, sauf très localement dans les cas de blessure, régénération, greffe. Mais il s'agit là d'un phénomène local, le reste des tissus gardant leur différenciation et leur gradient propre.

Les transplantations d'appendices avec leur base en territoire qu'on peut qualifier de "neutre", c'est à dire ne développant normalement aucun appendice, met en évidence le fait que le "territoire de régénération" est nécessaire à la survie de la greffe et que d'autre part, le régénérat est conforme à sa spécificité primitive et non à sa nouvelle situation.

Dans la compétition entre deux territoires à potentialités morphogénétiques différentes, après une sorte de "symbiose" entre les deux parties donnant naissance à une "chimère", c'est le territoire d'implantation qui prédomine.

La greffe est absolument liée à la régénération et se traduit par une manifestation de celle-ci. Elle nous permet de définir deux sortes de territoires.

—*les territoires "neutres"* sans potentialités morphogénétiques propres, mais qui peuvent réagir à l'action d'un transplantat à spécificité déterminée.

—*les territoires "negatifs"* sans potentialités morphogénétiques propres et incapables de réagir à l'activation traumatique de la greffe.

—*les territoires positifs ou territoires de régénération* qui ont une spécificité bien définie, spécificité dominante sur un territoire neutre.

Dans le cas de greffe, si le transplantat est placé en "territoire neutre" il se développe conformément à sa spécificité primitive indépendemment de sa nouvelle situation par rapport à l'organisme.

S'il est transplanté en territoire négatif, il n'y a aucune prise.

S'il est placé en territoire positif, la spécificité du greffon est sensible pendant la première mue, mais est "couverte" en quelque sorte par celle du territoire ou il est transplanté pendant la suite du développement. Si on met en compétition deux territoires à spécificités définies et différentes, le territoire prédominant est celui qui a gardé ses connexions normales avec le reste de l'organisme.

GENERAL AND FUNCTIONAL MORPHOLOGY

MOULT AND INTERMOULT EVENTS IN THE EPIDERMIS

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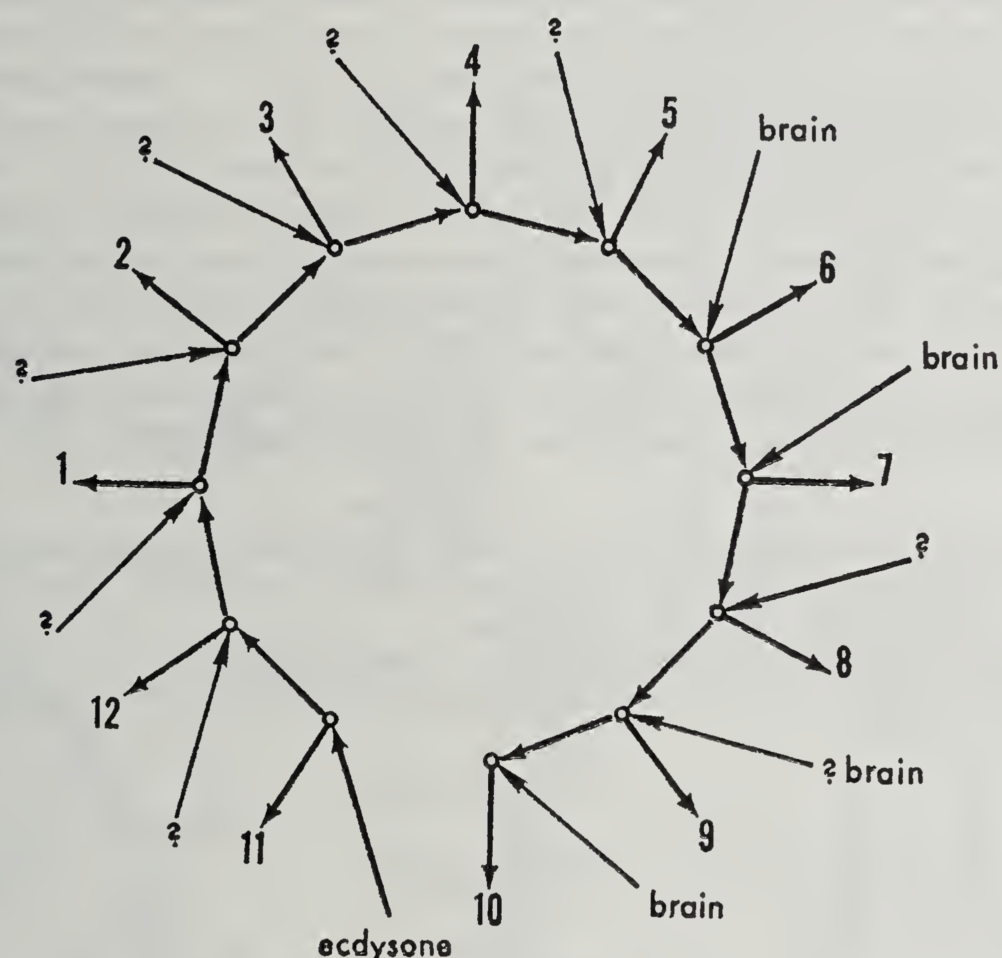
Classical studies in insect endocrinology have demonstrated that moulting is initiated by the prothoracic glands controlled from the brain (5). The choice of much experimental material has restricted research to the mechanism by which quiescent cells become active, and has resulted in a tendency to ignore the many discrete synthetic events taking place in the epidermis during a stadium. The most important of these events are outlined in Fig. 1. Some of them, for example the secretion of wax and the deposition of the endocuticle, take place in both the moult and intermoult periods. The problem therefore arises whether the activities of the epidermal cells are under the continuous control of a hormone or hormones. Do changes



1 Cuticulin secretion
2 Inner epicuticle formation
3 Activation of the moulting fluid
4 Cuticle resorption
5 Endocuticle deposition
6 Ecdysis and plasticity
7 Harding and darkening
8 Wax secretion
9 Endocuticle deposition
10 Wax secretion
11 Ecdysial membrane formation
12 Moulting gel

Fig. 1. The control of epidermal syntheses. (*a*) the numbers 1-12 represent the syntheses which an epidermal cell undertakes in a moult/intermoult cycle. Each event (o) probably has some intrinsic factor relating it to the previous event and may be modulated or controlled by external factors (arrows). Syntheses 11, 12, and 1-8 are moulting events. Syntheses 9 and 10 occur in the intermoult.

in the rate and kind of synthetic activity of an epidermal cell depend upon changes in concentration and type of hormone, or does a single moulting hormone merely trigger the start of a series of events within a target cell which are then further regulated by factors within the cell? The two extreme hypotheses are represented in Figs. 2(1) and 2(2). The most probable solution is the compromise shown in Fig. 2(3) in which different events are controlled by a meshwork of intrinsic and extrinsic factors.

Two intermoult activities of the epidermal cells have been studied in the larva of *Calpodes ethlius*, Lepidoptera, Hesperiidae. Both wax secretion (3) and endocuticle deposition are stopped by ligation of the head, a procedure which does not block moulting. From this and other experiments it seems probable that these intermoult events are not controlled by ecdysone alone.

The activities of the epidermal cells fall naturally into two groups in time, moult (syntheses 11, 12, 1-8) and intermoult (syntheses 9, 10). We might therefore expect two periods of preparation on the part of a cell. Evidence in support of this hypothesis has come from autoradiographic studies of RNA synthesis (4). There are two peaks of RNA synthesis, one post-moult and one pre-moult. The former is not blocked by ligation and is triggered off at ecdysis or earlier. The latter corresponds to activation by ecdysone.

Fig. 3 shows the general scheme of control for each of the syntheses mentioned in Fig. 1. If we consider ecdysone to initiate the sequence, then it begins with the preparation of the cell for protein synthesis, in particular the formation of RNA. Immediately following and partially coincident with this preparation of the cell, the first secretory syntheses occur—ecdysial membrane formation and moulting gel secretion (syntheses 11, 12). Most of the syntheses occurring at moulting appear to be part of the ecdysone initiated sequence and cannot be blocked by ligating the head. However, in later events in some insects even syntheses (6 and 7) directly connected with moulting may be extrinsically determined (1), and although the preparation of the cell for intermoult activities (the immediate post-moult phase of RNA synthesis) may be one of the last effects of ecdysone stimulation in the previous stadium, the control of the final synthetic events in the intermoult is extrinsic.

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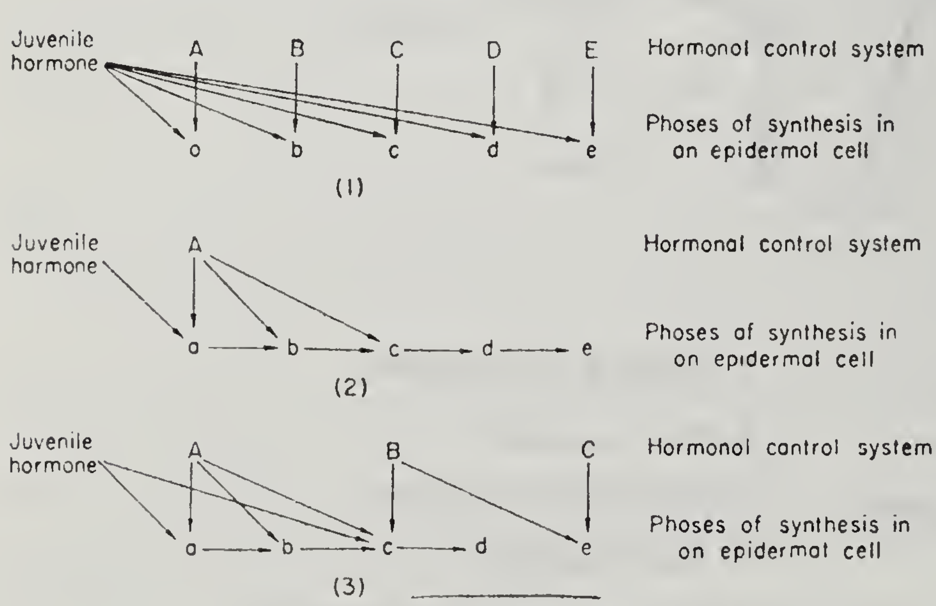

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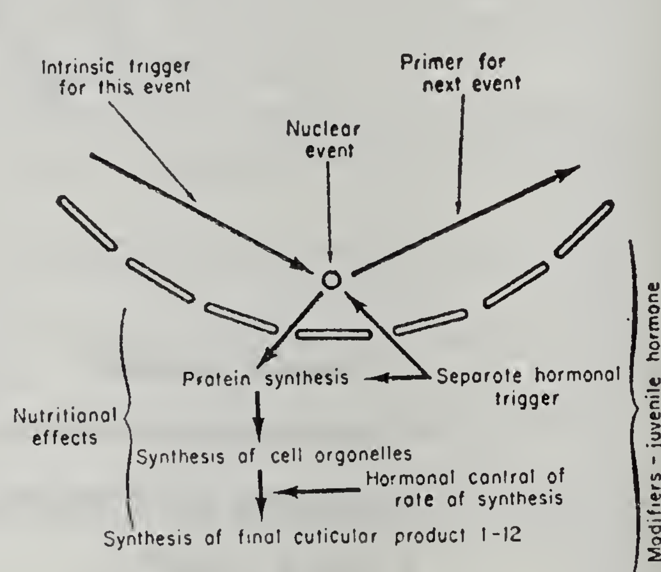

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Figs. 2 and 3. (2) The problem of the control of epidermal syntheses. ABCDE are possible controlling factors; *abcde* are phases of synthesis. In its simplest form the problem is one of extrinsic 2(1) versus intrinsic control 2(2). The most probable type of answer is to be found in (3) with an interplay of several factors. *A* would correspond to the initiation of the moulting sequence by ecdysone. (3) A model scheme for the control of each of the synthetic events outlined in fig. 1.

HABROCERUS CAPILLARICORNIS GRAV. COLEOPTERE STAPHYLINIDE SANS EDEAGE

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Si l'on examine un *Habrocerus capillaricornis* ♂, on constate que cet insecte a un abdomen de 5 segments visibles au lieu de 7 chez la ♀, de même que chez tous les Staphylinides ♂ et ♀. Chez *H. c.* ♂, l'abdomen finit avec le propygidium dont le bord postérieur porte un étroit liseré membraneux blanchâtre comme il est de règle chez les Staphylinides ailés. Le pygidium et le segment génital bien visibles chez la ♀ manquent chez le ♂. Deux lanières noirâtres croisées dépassent seules le sommet du propygidium (fig. 1A).

Si l'on dissèque un *H.c.* ♂, on constate que le canal éjaculateur venant des testicules se dilate brusquement à l'intérieur de la cavité générale de l'abdomen pour constituer un sac allongé densément garni de très petites phanères et d'écailles épineuses noires imbriquées, portant en outre une série de fortes épines noires (fig. 2A). Ce sac va déboucher au dessous et

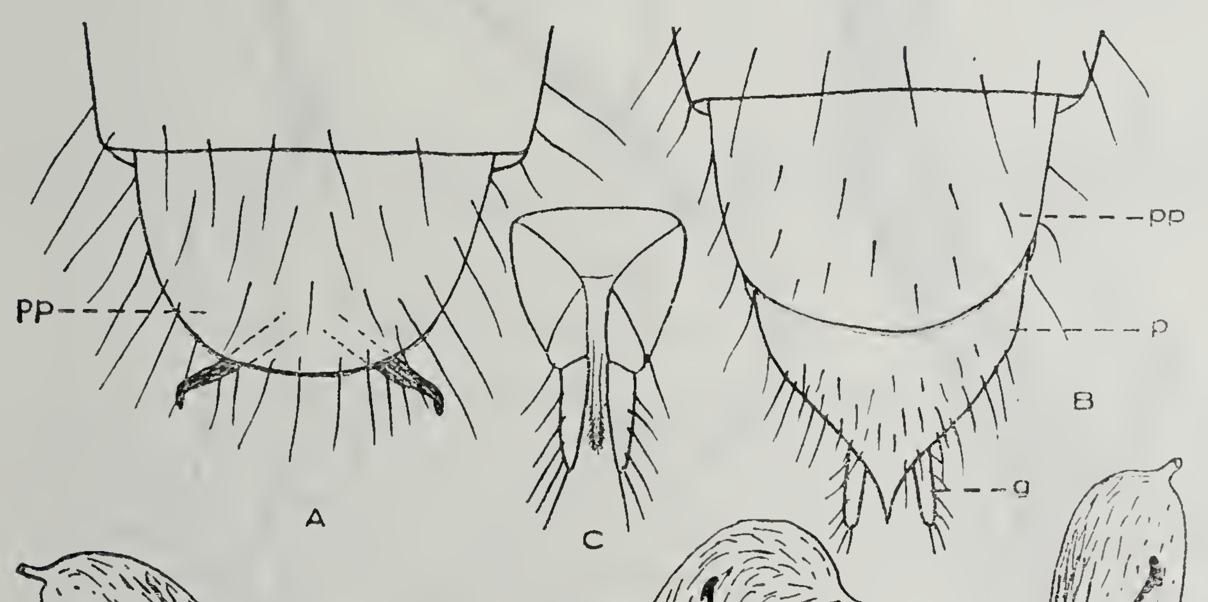

Fig. 1.—*A:* Sommet de l'abdomen vu de dessus de *Habrocerus capillaricornis* grav. mâle; *pp.* propygidium. *B:* Sommet de l'abdomen vu de dessus de la femelle; *pp.* propygidium; *p.* pygidium; *g:* segment génital. *C:* Segment génital femelle vu de dessous. *D:* Organe copulateur mâle vu de dessus. *E:* Le même vu de dessous. *F:* Le même vu de profil.

un peu en retrait de l'anus, à l'extrémité d'un petit segment où l'on peut reconnaître un sternite portant 5 ou 6 petites soies, deux pleurites dépassant le sommet du sternite, à leur extrémité incurvés vers le haut et finement pubescents, et enfin un tergite membraneux sauf sur ses bords antérieur et latéraux où se voit une bandelette sclérifiée (fig. 2A).

Ce petit segment est embrassé par un organe dans l'ensemble en forme de pince, où l'on peut reconnaître une plaque sternale sur laquelle s'articulent 2 appendices à base épaisse et à sommet grêle, portant chacun 3 longues soies (fig. 1E). Du côté dorsal, la base de ces appendices est unie par une pièce transversale en forme de V très ouvert, fortement sclérifiée (fig. 1D).

Cet étrange organe copulateur avait été interprété par Jeannel et Jarrige (1949, *Biospeologica* LXVIII, 347) comme un édéage aberrant du type "en cavalier". Mais ils n'avaient pas remarqué qu'il manquait 2 segments à l'abdomen.

Le petit segment au sommet duquel s'ouvrent l'anus et le pore génital ne saurait en aucune façon être considéré comme le lobe médian d'un édéage car jamais le rectum n'est logé

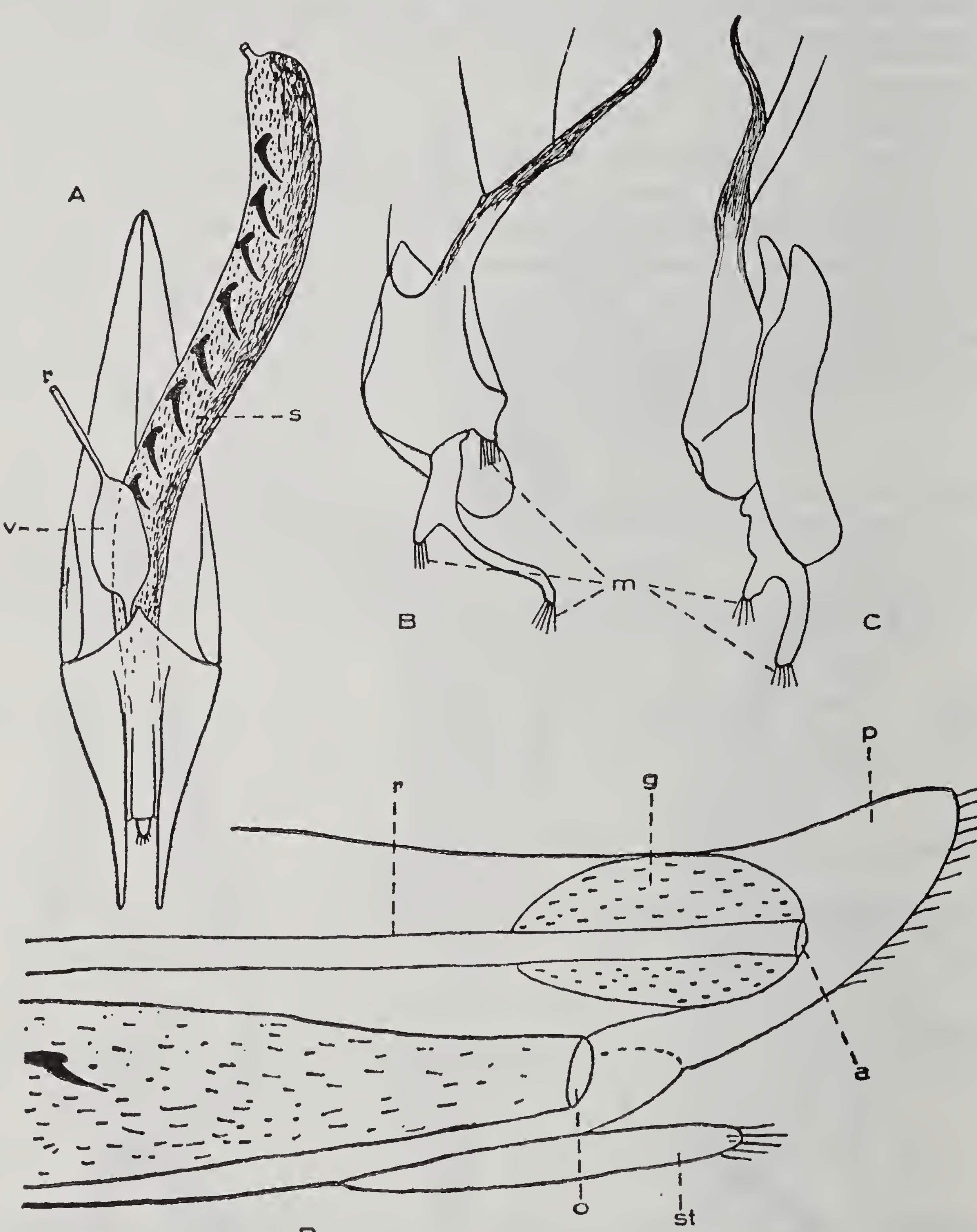

Fig. 2.—*A:* Segment génital vu de dessus; *s:* sac génital; *v:* vésicule anale. *B:* Branche gauche du forceps vue de dessous. *C:* La même vue de profil; *m:* muscles. *D:* Coupe longitudinale schématique du sommet du segment génital; *a:* anus; *g:* glande anale; *r:* rectum; *o:* orifice génital; *st*: sternite; *p:* pleurite.

dans l'édéage. Or chez *H. c.*, le rectum traversant à son extrémité une glande anale est très nettement distinct à l'intérieur du segment, au dessus des voies génitales, et l'anus se situe au sommet de ce segment, au dessus et un peu au-delà du gonopore.

Ce segment n'est donc pas un lobe médian d'édéage, maix un véritable segment génital (Urite IX) et la position relative de l'anus et du gonopore est normale.

Quant à l'organe embrassant la base de ce segment génital, je le considère comme un Urite VIII (pygidium) modifié. Sa plaque ventrale correspond au sternite, les longs appendices articulés sur cette plaque peuvent être regardés comme des pleurites et la pièce dorsale en V ouvert comme un tergite.

Si l'on étudie la musculature, on constate qu'il n'y a aucun muscle permettant à l'Urite IX de coulisser dans l'Urite VIII, ce qui confirme qu'il ne s'agit pas d'un édéage du type "en cavalier". Par contre, des muscles fixés d'une part sur la plaque sternale et sur la pièce dorsale de l'Urite VIII et d'autre part sur les apophyses basales des appendices du même segment, permettent à ceux-ci de fonctionner comme un véritable forceps soit pour ouvrir les voies génitales ♀, soit pour saisir le spermatophore et le porter dans les voies femelles.

H. c. est donc un Coléoptère dont le mâle n'a pas d'édéage, mais un très curieux organe copulateur formé à partir du pygidium.

A NEW TYPE OF COMPOUND EYE IN LEPIDOPTERA, WITH SOME REMARKS ON MUELLER'S MOSAIC THEORY

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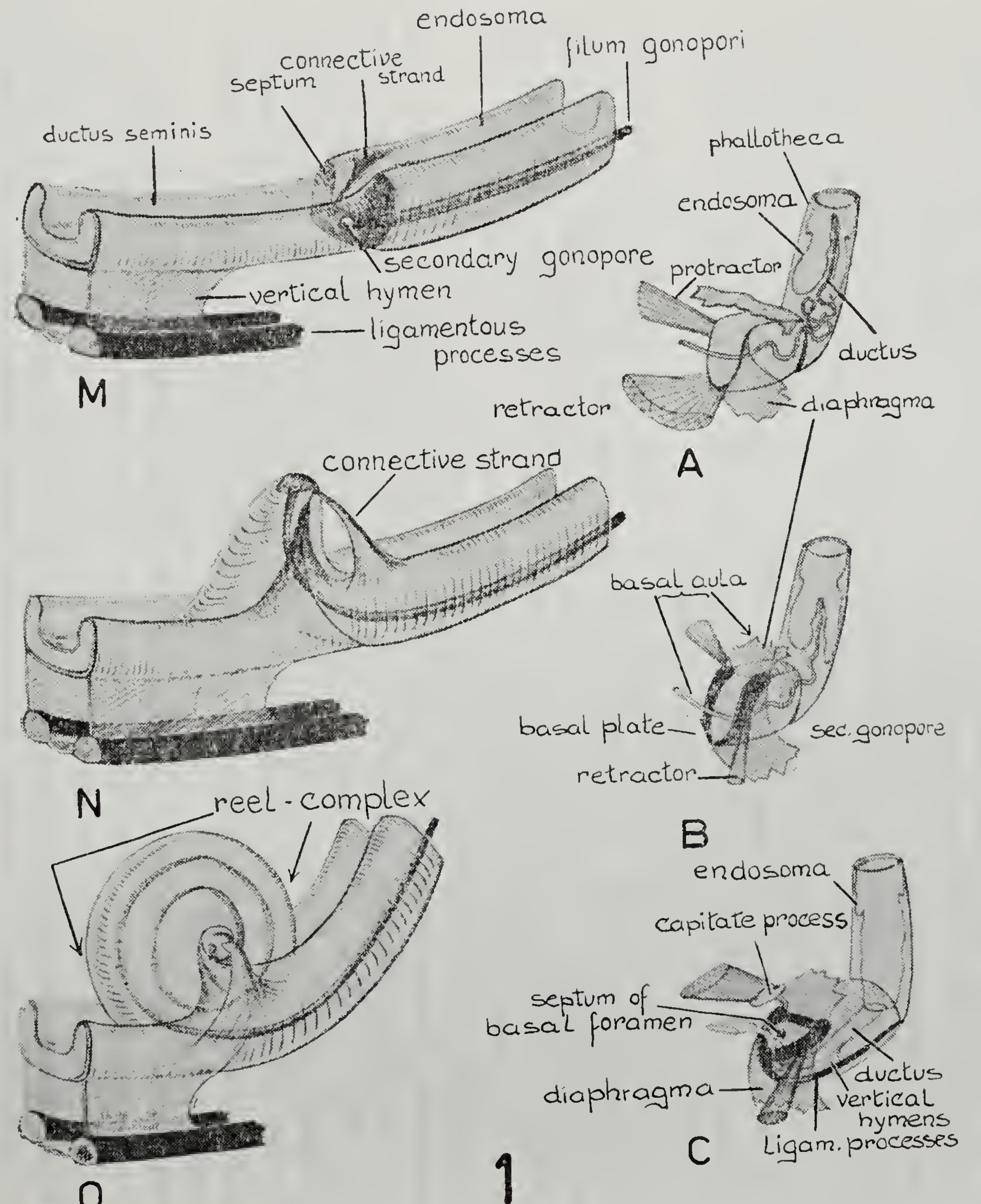
The true compound eye of Insecta, excluding the agglomerated eye, has as a rule hexagonal facets of uniform size; there are exceptions such as some Tabanid and dragon flies and a species of moth, *Psilogramma increta*. The author discovered that, in the case of butterflies of the genus *Leptidea* (Pieridae), there are two different sizes of deformed hexagonal facets. On the entire surface of the eye the two kinds intermingle in a somewhat irregular fashion, the smaller facets having a diameter of almost 60% that of the larger ones. As might be expected, the sizes of the inner parts like the corneagenous cells and the crystalline cones, vary correspondingly. This form of compound eye is characteristic of all species of *Lepidea* examined: *L. duponcheri*, *L. morsei*, *L. sinapis*, *L. gigantea*, and *L. amurensis*.

Müller's mosaic theory (1826), is still accepted in almost every text-book of Biology, Ophthalmology and Entomology. Our experiments show that the image is formed in each ommatidium independently. Therefore the retinular sense cells in an ommatidium receive each one part of this image from which a different impulse will be propagated inwards. The neurons in an ommatidium, 8 in this instance, unite with the neurons from other ommatidia, and likewise the nerve cords from several ommatidia construct a nerve bundle.

In Lepidoptera three different types of nerve bundles occur. In type 1, found in the eyes of members of the Papilionoidea, the bundles are very stout and each nerve bundle is compactly coiled. Type 2 is found in the eyes of almost all species of Lepidoptera (except those of the Papilionoidea); here the nerve bundles are longer and their distribution is less compact. In type 3 the nerve bundles are branched, each branch passing straight into a retinular sense cell of an ommatidium; this type occurs in the eyes of skippers (Hesperiidae) and of diurnally active Sphingid moths.

As a rule there are two chiasmatic crossings of the nerves, the first in the periopticon, the second in the epiopticon region. But this phenomenon is not universal in the eyes of Insecta because the eyes of the more primitive insects have no evident chiasmata. The nerve bundles, no matter what their type, of adjacent ommatidia perceive an image coming from the same direction in the environment. Therefore, the well developed eye can perceive an image with many nerve bundles simultaneously. The image seems to be composed of the sum of the stimuli of the neurons composing each single bundle of the nerve cord.



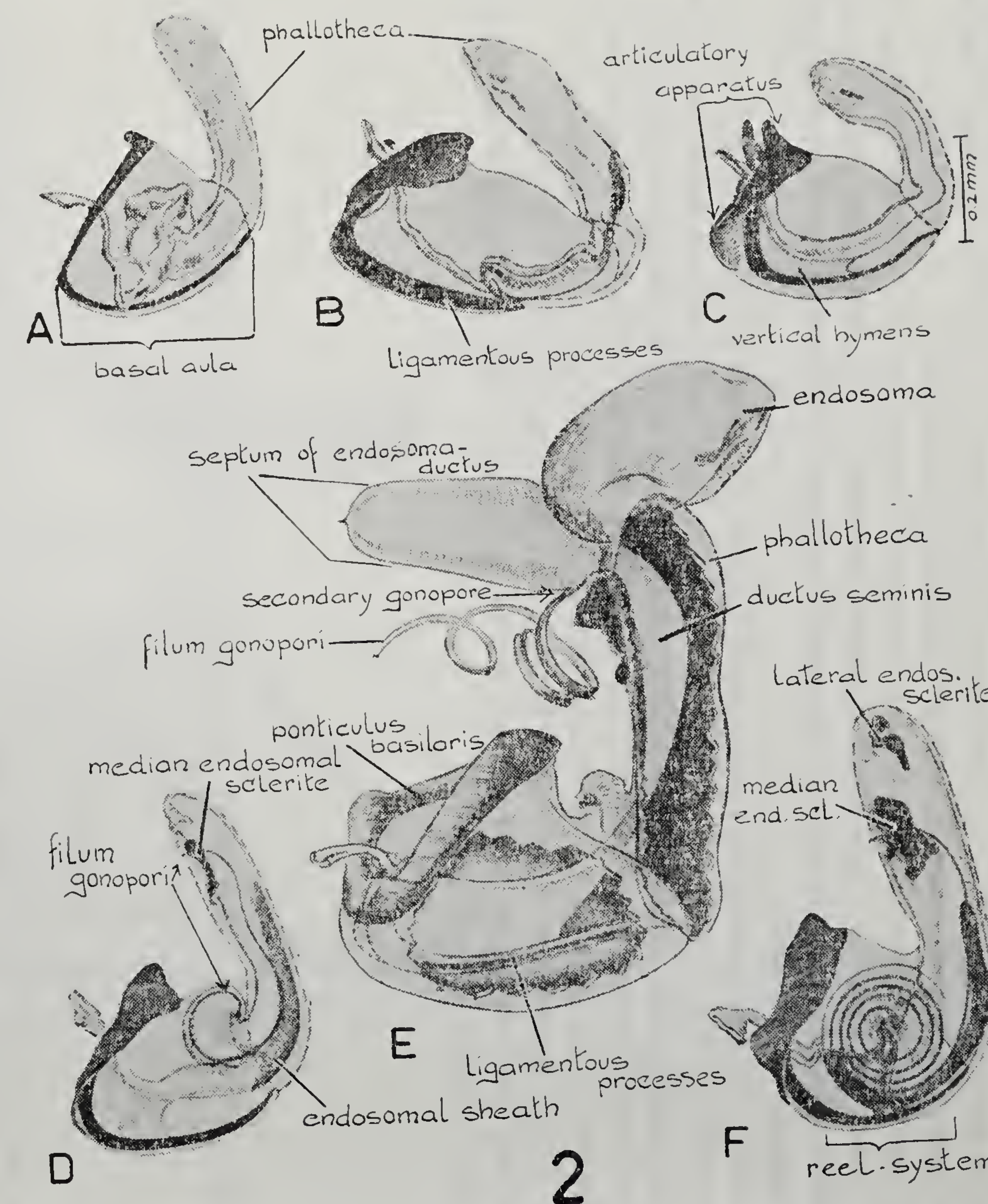


Fig. 1. A-C, diagram of phallus; A, amphibicorisan type; C, primitive leptopodoid type; B, hypothetical intermediate type. M-O, stages in the development of the reel-system. Fig. 2. Leptopodoid phalli, left lateral view; A, *Leotichius speluncarum* (*Leotichiidae*); B, *Leptopus marmoratus* (*Leptopodidae*); C, *Aepophilus bonnairei* (*Saldidae*); D, *Chiloxanthus pilosus* (*Saldidae*); E, *Ch. pilosus*, inflated (additional manual pressure on the specimen fixed in copula has effected a hyper-extension of the terminal septum); F. *Salda littoralis* (*Saldidae*).

THE FUNCTIONAL MORPHOLOGY OF THE LEPTOPODOID PHALLUS: A CASE OF RECTILINEAR EVOLUTION IN SALDIDAE (HEM.-HETEROPTERA)

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The Leptopodoidea contains the families: Omaniidae, Leotichiidae, Leptopodidae, Saldidae. Species of *Saldidae* mate side by side due to a lateroanterior grasping plate on the males' abdomen. *Omania* has an homologous pincers structure also but of a quite different type. *Leptopus marmoratus* copulates side by side although structural adaptation to this behaviour has not developed. Two morphological questions concerning the intromittent organ proper are discussed here.

The phallotheca in leptopodoids is connected to the stirrup-shaped articulatory apparatus by means of a large membranous compartment, here termed *basal aula* (fig. 2A). This phallic unit is of great phylogenetic importance in Heteroptera. The amphibicorisan phallus represents in all respects the most primitive condition in Heteroptera. Fig. 1 illustrates our interpretation of the origin and development of the more evolved articulatory apparatus (C) and basal aula derived from the amphibicorisan type (A). The phallus base represents originally a simple trough-shaped excavation of the diaphragma, gradually becoming thicker, the parameres attached directly to the anterior dorsal edges of the trough. The muscular operating mechanism is simple. Body fluid finds ample entrance to the phallus and endosomal inflation is easily caused by manual pressure on the abdomen. No bulbus ejaculatorius is present, the thin sperm duct running free from beginning to end. All these characters apply to members of the main amphibicorisan stem. The following stage is: the development of basal plates or stapes by sclerite insertions lateral to the U-profile (B); dorsal closure of the aula by attachment of the membrane to the trough sides and to the later developed ponticulus basilaris; partial basal foramen closure by septum; ductus attached to the stirrup; pro- and retractors centralised on special holders; development of ligamentous processes, connected with the now shortened, widened, gutter-shaped sperm duct by means of two vertical membranes, here termed *vertical hymens* (C). We now arrive at the basic pattern for the leptopodoid organ (approaching *Aepophilus*). Although the sperm duct has a different histological structure before and behind the basal foramen (Dr. Carayon, pers. comm.) it is questionable whether this difference concurs with the separation into ductus ejactulatorius and d. seminis. Considering the amphibicorisan condition, the structural differentiation is more likely to be secondary. The foregoing indicates that from the male genitalia it is impossible to place leptopodoids at the base of the amphibicorisan stem.

The second question to be considered here briefly (in more detail elsewhere) refers to the evolution of a complex structure within the basal aula of Saldidae (fig. 2 *c-f*). A progressive shortening of the ductus has involved the growth of a new structure, the *filum gonopori*, a grooved strip for the further transport of sperm. Both counteracting phenomena (shortening of the ductus lengthening of the filum) have led to the unique ductus-filum-endosoma complex, abbreviated to the "reel-system". Fig. 2 *d,f* shows this system in its simplest (Chiloxanthinae) and most complex form (Saldini). All intermediate types, constant for each species, are to be seen in the Saldidae. The dimensional construction of the reel is illustrated in fig. 1, *m,n,o*.

With the progressive development of this coiling many additional phallic structures appear and evolve. In fig. 2 *d* and *f* only a few of them are drawn. The known species of Saldidae show therefore an ideal rectilinear evolution so far as the genitalia are concerned.

THE GULA IN ADULT COLEOPTERA—A FUNCTIONAL INTERPRETATION

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An attempt has been made to explain the gular width of certain adult beetles in terms of the size of the head capsule and the arrangement of its musculature and endoskeleton. In many groups of beetles (e.g. Aphodiinae) the gular width to head width ratio remains approximately constant in species of increasing size, whereas in the Staphylininae it declines because

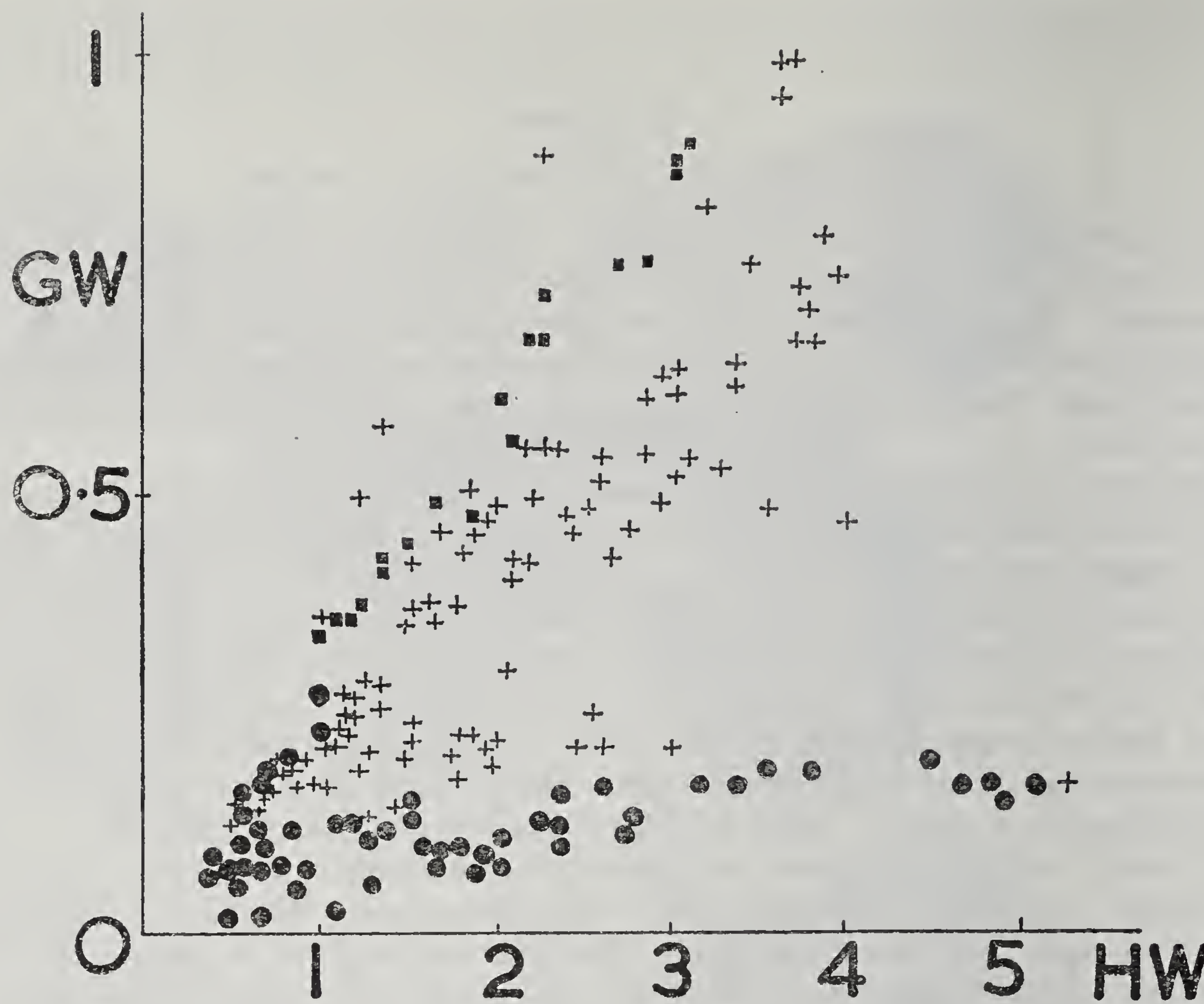

Fig. 1. Graph to show the relationship between average gular width (G.W.) and head width at the temples (H.W.) in certain species of Coleoptera. (Aphodiinae: squares; Staphylinidae: circles; Carabidae: crosses. Figures in millimetres).

the absolute width of the gula remains nearly constant (fig. 1). Thus in very large Staphylininae the gular sulci meet in the midline. It is suggested that this is due to a relative increase in the size of the mandibular adductors which is necessary to maintain the relative biting force in larger species, this being required for the penetration of tough prey. It is postulated that this need arises because if the head width were doubled, the volume (and weight) of the head would increase about eight times, whilst the cross-sectional area of the mandibular adductors would only quadruple. Ventrally, the mandibular adductors lie lateral to the gular ridges, and therefore the lateral parts of the head capsule are expanded in big species. This would explain the proximity of the gular sulci in large Staphylininae.

Most of the Staphylinidae in fig. 1 lie along an approximately straight line which includes Staphylininae, Paederinae and Aleocharinae. However, Tachyporinae lie above this line, and Oxytelinae below. In Tachyporinae the gular width to head width ratio behaves as in Aphodiinae, perhaps because of the relatively wide head capsule. The Oxytelinae examined were small species, but had gular width to head width ratios as small as in the largest Staphylininae. This suggests that the mandibular adductors need to be especially powerful, probably because *Oxytelus* includes burrowing species which have digging spines on the tibiae. This correlation between small gular width to head width ratios and predacious burrowing species is also seen in *Necrophorus* and in the Histeridae. Those Curculionoidea which have confluent gular sulci are entirely herbivorous, but the mandibles are often specialised to deal with very hard materials and thus the adductors would have to be as large as possible.

Although many Carabidae are predators or scavengers the relationship between head width and gular width is in contrast to that of the Staphylininae (fig. 1). This may be accounted for by the different structure of the Carabid feeding mechanism. In Staphylininae, food is rotated and crushed in a pre-oral mill whilst the fluids are extracted. In Carabidae, large pieces of food are raked into the mouth by maxillary retraction brought about by the

stipital retractor muscle, which is absent in Staphylinidae. As the stipital retractors, like the labial muscles, lie on the head floor between the gular ridges, the proportions of the gula are similar in the majority of Carabidae. Exceptional species are included in the burrowing *Scarites* and the herbivous *Amara* and *Harpalus*. In many Adephaga, a midgular apodeme supports the labial muscles. This allows a vertical instead of a horizontal arrangement of the muscle origins and may reflect the need of many species to reduce the relative gular width to accomodate the large mandibular adductors.

(To be published at length in the Proceedings of the Zoological Society of London).

LES LARVES DE TRICHOPTERES HYDROPTILIDES MANGEUSES DE SUBSTRAT

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Les larves des Hydroptilidae peuvent être séparées en deux groupes assez distincts, suivant leur habitat et leur mode de vie.

Celles du premier groupe (*Hydroptila*, *Agraylea*) vivent, soit en eau courante, soit en eau stagnante, accrochées à des algues filamenteuses; elles se nourrissent des contenus cellulaires de ces végétaux; leurs pattes de la première paire ont des pinces tibio-tarsales, qui leur permettent de saisir les algues. Leurs fourreaux sont soit aplatis latéralement, soit de section presque circulaire.

Les larves du deuxième groupe (*Stactobia*, *Leucotrichia*) ne s'observent que sur les pierres des cours d'eau rapides, voir même sur le front des cascades, ou sur les rochers suintants. Elles sont dépourvues de pinces tibio-tarsales et leur fourreau est presque toujours déprimé dorso-ventralement et aplati du côté du substrat. Elles se nourrissent de diatomées et de particules raclées sur la pierre devant elles.

Des larves de *Stactobia*—on connait actuellement 10 espèces de ce genre en Europe—n'ont été observées jusqu'ici que sur des rochers suintants, dans l'habitat pétrimadicole; leur fourreau a deux ouvertures circulaires ou presque.

Les larves des *Stactobia* sont caractérisées par la présence, sur chacun de leurs segments abdominaux II à VI, d'une plaque tergale "ajourée" dans sa partie médiane.

Or j'ai découvert sur des pierres, dans un ruisseau de l'île de Majorque, des larves de *Stactobia mallorcensis* qui se trouvaient toutes à plusieurs centimètres de profondeur. Ces larves fluicoles de *Stactobia* se distinguent des larves madicoles de toutes les espèces précédentes par la forme particulièrement grêle de leurs pattes. Le fourreau des larves de *St. mallorcensis* est remarquablement lourd et incrusté de calcaire et les deux premiers segments abdominaux ont des expansions latérales.

Aux Etats-Unis, j'ai recueilli, dans des habitats madicoles typiques, des larves d'*Ochrotrichia confusa* (Morton) et d' *O. riesi* Ross, les premières dans les Appalaches, les secondes dans les Montagnes Rocheuses.

Les unes et les autres ont un fourreau très déprimé dorso-ventralement, recouvert de grains de sable, et s'ouvrant en avant et en arrière par une fente étroite; elles ont, comme les larves des *Stactobia*, des plaques abdominales ajourées. Elles ont le même type de nourriture que les larves des *Stactobia* et cependant elles ont une pince tibio-tarsale très nette. Il s'agit sans doute d'un organe vestigial. Celà semble confirmé par le fait que les larves de toutes les autres espèces d'*Ochrotrichia* que l'on connait sont du groupe *Hydroptila*; leur fourreau est déprimé latéralement et elles se nourrissent vraisemblablement d'algues filamenteuses.

Jusqu'ici, on ne savait rien concernant les premiers stades des *Allotrichia*. Le Dr. G. Marlier, de Bruxelles, a eu la grande amabilité de m'envoyer des larves d'*Allotrichia africana* qu'il avait recueillies au Congo sur la paroi rocheuse d'une cascade. Ces larves rhéophiles ont un fourreau, entièrement membraneux, peu différent de celui des larves de *Stactobia maculata*, et des plaques abdominales ajourées. Elles n'ont pas de pince tibio-tarsale, mais elles se distinguent de toutes les larves de Trichoptères connues jusqu'ici par les caractères suivants: leurs pattes, très trapues, ont le tibia et le tarse soudés.

DEVELOPMENT

MAJOR EVENTS IN THE FIRST THREE DAYS IN THE LARVAL LIFE OF THE HONEYBEE

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Female honeybee larvae show differing, characteristic patterns in respiration, growth, tissue composition, blood protein and corpora allata development, presumably as a result of different diets. Caste determination is progressive. The first 48 hours are relatively plastic. During the third day any regulative capacity is virtually lost.

Alterations of natural diets such as the addition of sugar to worker jelly to give a total concentration equivalent to that of royal jelly affect all developmental parameters referred to above.

Similarly, additions of water soluble acids which occur in higher concentration in royal jelly also alter developmental patterns. These acids are active at low concentrations, are growth inhibitors and appear to act antagonistically to the effect of sugar.

The effects of both sugar and water soluble acids are conditioned by larval age and stage of development.

Evidence for hormonal participation is shown by the histological changes in the corpora allata. These are influenced in turn by diet. During larval life the corpora allata seem to play a central role in mediating between nutrition and caste determination.

EGG-LIFE AND SYMBIONT TRANSMISSION IN A PREDATORY BUG, *MESOVELIA FURCATA* MS AND REY (HETEROPTERA, MESOVELIIDAE)

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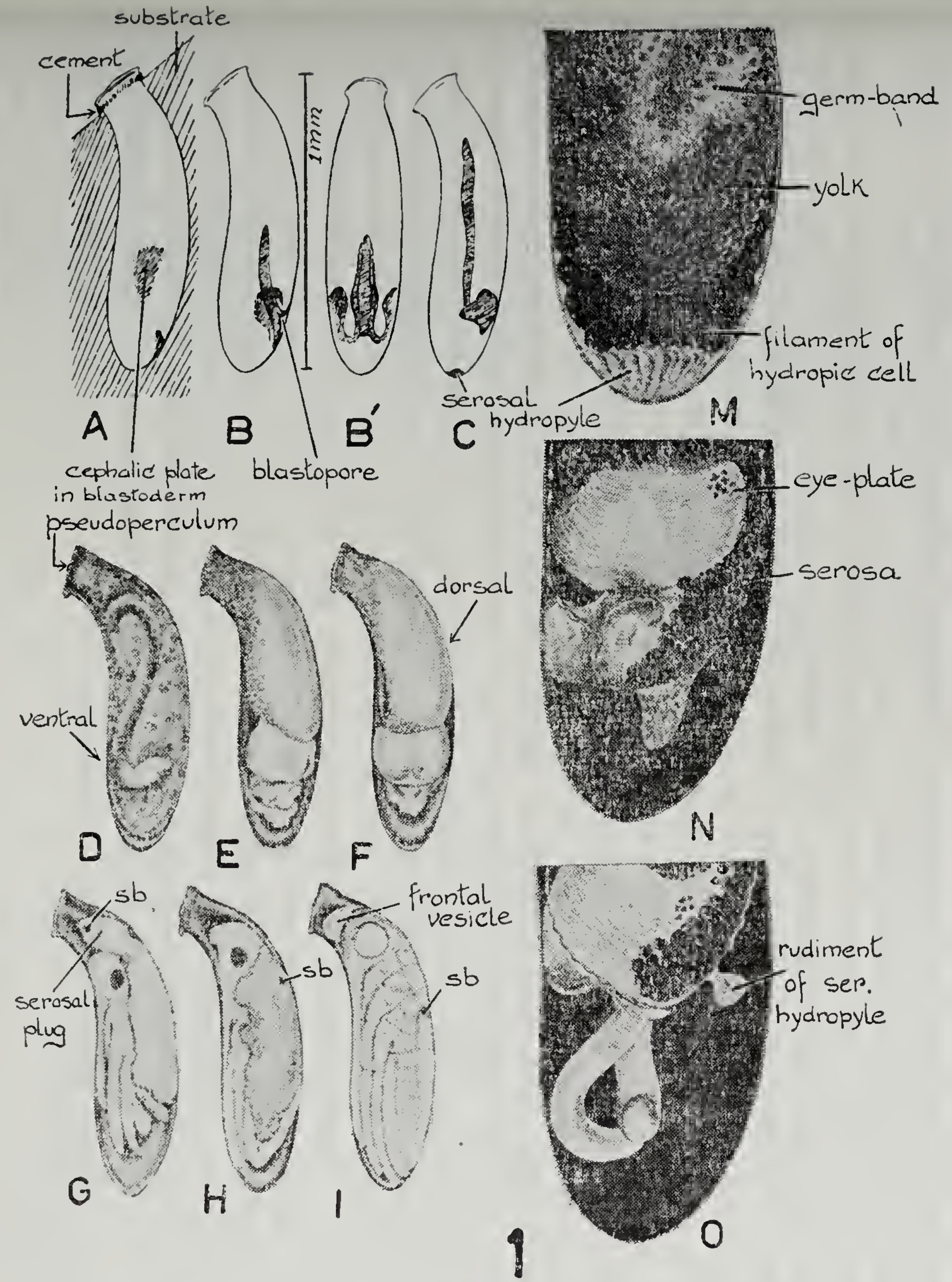
The egg of this 3 mm. long water-surface dweller is atypically embedded, its caudal pole pointing to the ovipositing female (as in Saldidae), and we can assume a 180° rotation of the egg before laying. The egg-shell has a pseudoperculum, a single micropyle, thin chorion (2·5 μ, 4× thicker in the cap), apparently without an aeroscopic inner layer. The eggs incubate and hatch successfully under both continually submerged or moist atmospheric conditions (10·5 days, 30°C). Invagination occurs dorsal to the posterior pole, ventrum of the germ-band facing ventral side of the shell, germ cells not separated from tail end (fig. 1A-C). Posterior pole occupied by a serosal hydropyle contiguous with the yolk. After the appearance of protocormic appendages the considerably retracted yolk column is contacted at its boundary by one elongate cytoplasmic filament per hydropic cell (fig. 1M). The subsequent lumen is probably water-filled before the substantiation of the serosal cuticle. This situation continues to blastokinesis when a longitudinal 180° embryo rotation (clockwise, seen from anterior) is followed by a ventral revolution. The hydropyle (as part of the contracting serosa) moves anteriad (fig. 1N,-O), being still visible sinistrally to the serosal plug. An active process (described elsewhere) resulting in the uptake of the plug to form part of the dorsal organ, is marked by increasingly intensive spasmodic contractions of a serosal cell-band, and a complete deformation of plug form proceeds visibly. As a consequence of these extra-embryonic beats, the yolk is pressed irregularly beneath the dorsal closure, the serosal plug retreats from the pseudoperculum and only now does a red sphere become visible in the top of the plug (fig. 1G). This body (dark granular symbionts embedded in red substrate) traverses both yolk and dorsal organ, reaching the anterior part of the stomach (fig. 1H, I). The body disintegrates during



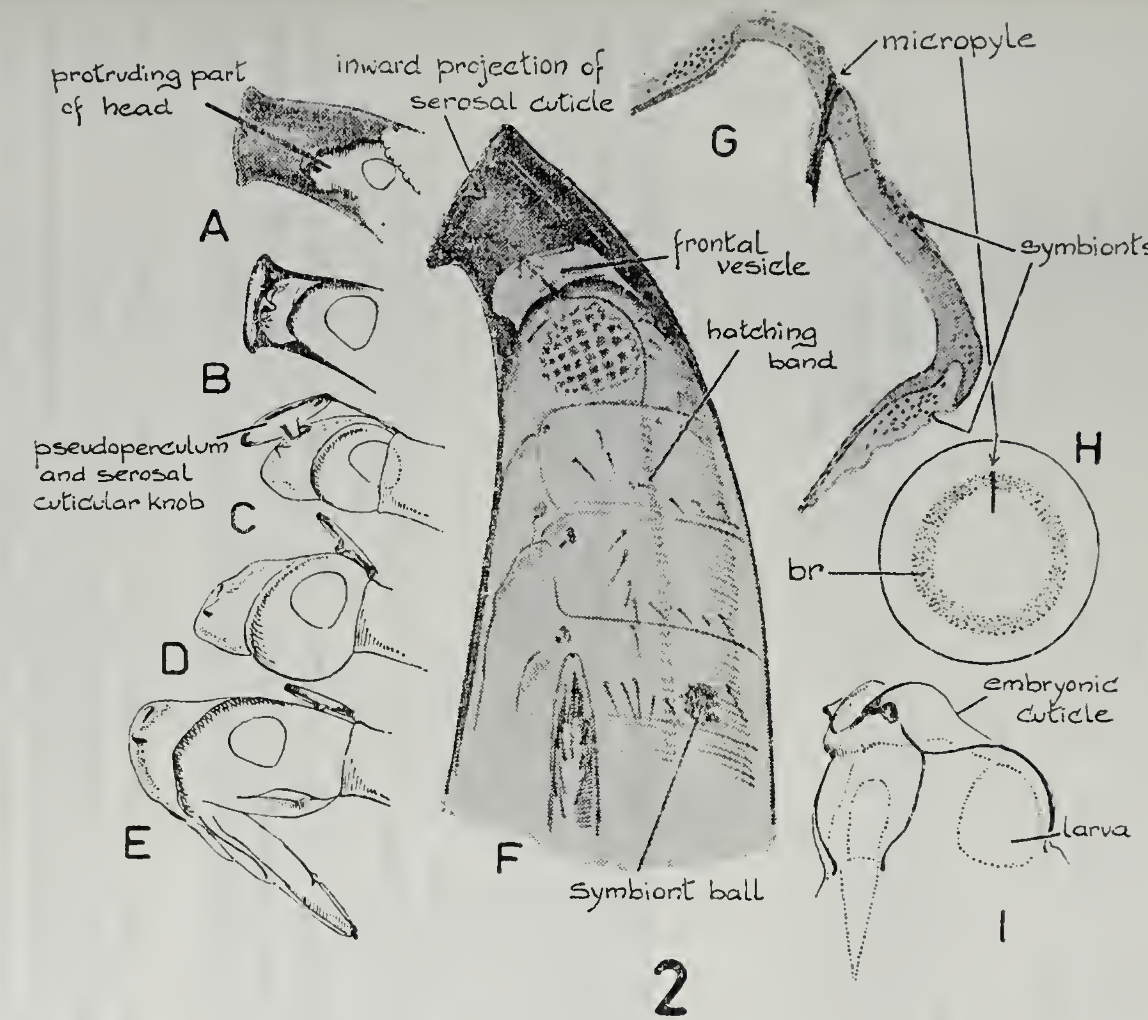


Fig. 1. *Mesovelia furcata,* egg. lateral view (B, dorsal view). A-I, gross embryology; sb, symbiont ball. M-O, location (M) and fate of serosal hydropyle during revolution of embryo (N, O).

Fig. 2. *Mesovelia furcata,* egg. F, full-grown embryo; A,B, formation of frontal vesicle; C-E, eclosion act, G, sagittal section through egg-cap; H, pseudoperculum and brown ring (br) beneath serosal cuticle; I, head frame and vesicle of embryonic cuticle.

hatching, but in the free larva the fragments recombine posteriorly in the mid-gut; definite fractioning occurs early in the same larval instar. The red fragments enclosing symbionts reappear only in the gravid female as mid-gut wall intercellular inclusions and also free in gut contents. The recently laid egg is tapped two or three times with the anus and in such eggs, rod-shaped organisms ($1 \times 2\ \mu$) occur around the pseudoperculum (fig. 2G) and we suggest that these contaminate the eggs via the micropyle before the serosal cuticle is secreted. Prior to blastokinesis a brown ring appears under the serosal cuticle, concentric with the pseudoperculum (fig. 2H), which disappears shortly and obviously represents the symbiont stock. Eclosion is effected by a permanent, turgid frontal vesicle of the embryonic cuticle; figure 2A-E shows its formation and structural adaptation to a central inner projection of the serosal cuticle.

ANALYSE DE LA CROISSANCE D'UN INSECTE A DIAPAUSE OBLIGATOIRE POST-EMBRYONNAIRE: INFLUENCE DE LA PHOTOPERIODE ET DE LA TEMPERATURE SUR LES STADES QUI PRECEDENT LA DIAPAUSE. (*GRYLLUS CAMPESTRIS* L. ORTH. GRYL.)

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Si le déclenchement des diapauses "facultatives" a fait l'objet de nombreux travaux, particulièrement en ce qui concerne leur déterminisme photopériodique (1), celui des diapauses dites "obligatoires" insensibles aux facteurs externes, y compris la photopériode, reste mal connu.

La diapause de l'espèce utilisée occupe l'avant-dernier stade larvaire, caractérisé par une évolution lente à toute température (*Gryllus campestris* (2)).

I.—*Influence de la photopériode sur le stade précédant la diapause.* Trois populations de grillons, élevés isolés, au stade précédant la diapause subissant à 30°C respectivement 8, 16 et 24 Heures de lumière par jour, évoluent très différemment. Le lot à 8H. mue très vite de façon homogène Les deux autres plus tardivement et avec un étalement accentué des mues dans le temps, maximum dans le cas de l'éclairement 16 H.

Le comportement de l'insecte est parallèlement modifié: il creuse une galerie dans le sol plus intensément en longue photopériode qu'en courte.

Ainsi dans la nature, pendant les longs jours d'été, le grillon creuse un terrier tandis que sa mue d'entrée en diapause est *différée.* Puis arrive une certaine valeur inférieure de l'illumination-atteinte d'une part du fait de la décroissance de la longueur du jour en Août-Octobre, d'autre part, de façon additive, par l'obscurité du terrier ou l'insecte séjourne une partie du temps -laquelle déclenche la mue d'entrée en diapause, amenant *des insectes d'âges variés au même stade à une même époque.*

II. *Determination de la durée du stade de diapause au cours de la vie larvaire.* Considérant comme critère la durée du stade de diapause à 30°C, et ne retenant que les individus à diapause normaux, on montre que la croissance à basse température (20°C) pendant une partie de la vie larvaire modifie la durée du stade de diapause. (Les cas sortant des normes habituelles, soit par suppression du dernier stade larvaire post-diapause, ce qui donne des individus aberrants de type "néoténique"; soit par suppression de la diapause elle-même suivie de modifications, morphologiques, ne sont pas présentés ici (2).

Les données montrent que quelque soit la souche et le régime lumineux, la durée moyenne du stade de diapause est *diminuée* par refroidissement des insectes de poids inférieur à 55 mg. (2° à 3° stade). Les lots dont le stade de diapause est plus court ont à la fois la vie larvaire la plus longue et le poids de début de diapause le plus élevé, exception faite du lot en éclairage d'hiver, ce qui indique probablement une accélération par les courtes photopériodes plus intense à 30°C qu'à 20°C.

CONCLUSION.—

Bien qu'ayant un caractére d'obligation inhérente au cycle de développement de l'espèce, la diapause se trouve:

1°) *synchronisée indirectement avec les saisons* grâce à une sensibilité particulière du stade qui la précède.

2°) *modulée par le regime thermique* subi dans le début de la vie larvaire,
ce qui revient à dire que les habituels facteurs de déclenchement des diapauses facultatives (température, photopériode) modèlent à l'évolution des saisons les diapauses obligatoires au moyen de régulations complexes, mettant en jeu un déplacement de la sensibilité aux facteurs externes vers les stades précédant la diapause.

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EVOLUTION DE L'HYPODERME ET MISE EN PLACE DE LA CUTICULE CHEZ LA LARVE DU LEPIDOPTERE *GALLERIA MELLONELLA* (L.) (PYRALIDAE)

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Le mode de fonctionnement des cellules hypodermiques banales a été suivi pendant la vie larvaire de *Galleria*. Ces cellules présentent un cycle sécrétoire qui s'étend sur deux stades successifs et que la mue permet de séparer en une période préexuviale (dernière moitié d'un stade larvaire) et une période postexuviale (première moitié du stade suivant). Cette période sécrétoire commence toujours après une phase mitotique et se termine avant la phase mitotique suivante.

Période préexuviale. Elle montre que la formation du tégument se réalise cellule par cellule et que chaque cellule élabore trois séries de matériaux dont deux ont des structures et des colorabilités provisoires (stries verticales incolores du matériel exocuticulaire, couche granuleuse et rouge du matériel endocuticulaire, avec la triple coloration de Mallory) qui seront remplacées par les structures et les colorabilités définitives juste avant l'exuviation (structure homogène et rouge de l'exocuticule, strates bleues et parallèles à l'hypoderme pour l'endocuticule). La mise en place cellule par cellule est soulignée par l'existence d'un important cône cytoplasmique dont dépend la formation des zones d'exocuticule ou sclérites cellulaires qui demeurent toujours indépendants les uns des autres. Les matériaux endocuticulaires, au contraire, fusionnent et forment une endocuticule continue. Par contre, le matériel épicuticulaire d'emblée homogène et rouge au Mallory, semble acquérir très vite sinon directement la structure de l'épicuticule définitive.

Période postexuviale. Le cycle sécrétoire se poursuit par un apport de matériaux supplémentaires. Grâce aux cônes cytoplasmiques, on peut comprendre comment l'exocuticule et l'endocuticule peuvent augmenter de volume en recevant des matériaux en même temps et, indépendamment sans modifier le schéma initial établi lors de la période préexuviale. Enfin, la mise en place de ces structures nous montre comment la croissance qui se produit au cours de la période postexuviale, peut se réaliser sans modifier les différents rapports morphologiques. En effet, il y a déplissement de l'épicuticule, écartement des zones d'exocuticule, et étirement de l'endocuticule et de l'hypoderme.

Conclusion. Cette étude montre l'importance d'une sécrétion cellule par cellule dans l'établissement du relief du tégument larvaire.

Elle démontre que l'exocuticule est sécrétée indépendamment de l'endocuticule et qu'elle ne provient pas d'une modification de celle-ci mais d'un matériel préexistant. Les zones indépendantes d'exocuticule restent liées aux cellules correspondantes par des cônes cytoplasmiques encore visibles sur le tégument définitif.

Elle prouve que les strates de l'endocuticule ne sont pas formées en tant que telles à la surface des cellules hypodermiques puisqu'elles proviennent d'un matériel élaboré antérieurement et possédant une structure propre. Enfin, les modifications de structures se réalisant avant la mue, montrent que l'aspect lamellaire de l'endocuticule n'est pas dû à l'étirement provoqué par l'exuviation ou par les phénomènes de croissance de la période postexuviale.

SUR QUELQUES PULVINARIINI (HOMOPTERA, COCCOIDEA) DU MIDI DE LA FRANCE

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I.—Nous avons observé et élevé quatre Pulvinaires habitant le Sud-Ouest de la France (région de Toulouse). Elles se développent normalement dans les conditions naturelles et font partie de la faune locale indigène ou importée.

Pulvinaria oxyacanthae (L.) 1758. Elle ne se trouve que sur *Crataegus*, en pleine nature comme dans les jardins. La larve femelle se développe en quatre stades; l'éclosion a lieu début juin, la première mue début juillet, la deuxième fin août, la troisième mi-septembre. Les mâles nombreux fécondent les femelles adultes qui migrent alors sur les jeunes branches où elles passent l'hiver. La ponte se fait mi-mai. L'ovisac de type rond contient 2,800 œufs. Les larves peuvent vivre sur bois.

Chloropulvinaria floccifera (Westw.) 1870. Celle-ci est plus connue et plus polyphage; elle se trouve dans les jardins sur plantes à feuillage persistant, spécialement *Evonymus japonica* Thunberg. Le cycle dure normalement un an mais peut etre réduit en serre. La femelle se développe en trois mues: la première a lieu mi-août, la deuxième en octobre, non suivie de migration, la troisième en avril. Les mâles sont exceptionnellement présents, au printemps seulement. La ponte commence en mai; l'ovisac est linéaire et recouvre 1,100 œufs. Tous les stades vivent sur feuilles.

Eupulvinaria hydrangeae (Stein.) 1946. Elle est polyphage et se nourrit au dépens de plantes à feuilles caduques de jardins (*Tilia vulgaris* HAYNE, *Hydrangea Hortensia* SIEB . . . .) et de zones forestières (*Acer campestre* L.). Le développement se fait comme pour la précédente espèce en trois mues mais les L3 descendent sur bois en novembre.

Les femelles pondeuses migrent sur feuilles avant de sécréter un ovisac cannelé qui recouvre 2,800 eufs. Il n'y a jamais de mâle.

Neopulvinaria imeretina Hadz. 1955. Elle a la même répartition régionale que *Chl. floccifera* (jardins et friches de banlieue), hébergée par divers hôtes dont *Ampelopsis quinquefolia* L., *Vitis vinifera* L. et des *Vitis* américains. La femelle n'a que deux mues: la première a lieu fin Juillet, la deuxième fin Août. Les femelles adultes fécondées par les mâles très nombreux, hivernent sur bois après migration descendante. Elles croissent jusqu'en juin et sécrètent un gros ovisac rond qui recouvre 8,600 œufs. Les larves vivent sur feuilles.

II.—En outre nous avons utilisé un caractère morphologique stable des larves néonates pour aider à la distinction des espèces. Nous opèrons sur des montages faciles à réaliser car ne nécessitant qu'une seule manipulation: d'un bain au chloralphénol au milieu de montage (gomme au chloral de FAURE). Nous mesurons la longueur moyenne (L) de la boucle descendante de la crumena et éventuellement, celle de la boucle remontante (l). C = L + l est la "*longueur crumenale approchée*" exprimée en microns. De plus nous évaluons en % de C les valeurs de L et l.

Les espèces précédemment citées ont les types suivants:

	C (microns)	(L + l) %	*Boucle*
P. oxyacanthae	300	60 + 40	large—remontante
Chl floccifera	190	69 + 31	moyenne—peu remontante
E. hydrangeae	150	100 + 0	non remontante
N. imeretina	137	100	absente

LES PREMIERS ETATS DES COLEOPTERES AQUATIQUES DE LA REGION ETHIOPIENNE

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Jusqu'ici on connaissait assez peu les premiers états des Coléoptères aquatiques de la région éthiopienne.

Grâce à l'examen de nombreux matériaux provenant de divers territoires africains et à des récoltes personnelles poursuivies de la Guinée au Cap et à Madagascar, nous fournissons depuis 1961 une nouvelle contribution dont nous donnons ci dessous un bref aperçu.

La diagnose reste en principe limitée au genre; les formes étudiées appartiennent aux familles des Haliplidae, Dytiscidae, Gyrinidae, Hydrophilidae (*sensu lato*), Helodidae, Eubriidae Dascillidae (*Eubrianax*), Ptilodactylidae, Psephenoididae (Psephenoidinae Hinton), Dryopidae (*sensu lato*), Lampyridae, Chrysomelidae, Curculionidae.

Dans notre étude, descriptions et synopsis sont accompagnés de remarques et nous signalons quelques faits remarquables:

Dytiscidae—Les larves madicoles *Africophilus*, courant sur les rochers humides ont pattes et cerques sans soies natatoires.

Hydraenidae—La larve, également madicole, du groupe *Prosthetops* est pourvue de branchies latérales abdominales segmentées.

Hydrophilidae—A signaler qu'une larve inédite: Hydrobiinae genus A, offre une differenciation "inversée" des mandibules, la mandibule droite étant suceuse.

Helodidae—Biologie variée: larves lénitiques, des phytothelmes, lotiques et madicoles avec adaptations correspondantes; une larve de Guinée, madicole, est "psephenoide" et une larve des *Ravenala* de Madagascar, trés déprimée, a des pattes a griffes aplaties munies de soies natatoires. Les nymphes sont attachées a l'exuvie larvaire par des organes spéciaux: mamelons anaux.

Eubriidae—Larves aquatiques ou madicoles, les dernières parfois à facies particulier (*Afroeubria hygropetrica*).

Dascillidae (*Eubrianax*)—La face ventrale des nymphes possède des bourrelets adhésifs.

Dryopidae—Sauf une exception, les larves des Potamophilinae sont xylophages; les larves des *Omotonus* seules sont microphages, la nymphose ayant lieu sous l'eau, la nymphe, sans filaments pronotaux, attachée par les cerques à l'exuvie larvaire. Les larves des *Potamodytes* peuvent nager en utilisant comme propulsion le mouvement des branchies anales.

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SECTION 3.—PHYSIOLOGY AND BIOCHEMISTRY

The following papers were read but the authors did not wish for publication in these Proceedings:

Clements, A. N. (U.K.). The metabolism of isoprenoid compounds in insects.

Horridge, G. A. (U.K.). Neurons in the locust brain and optic lobe.

Kenaga, E. (U.S.A.). A new group of insect reproductive inhibitors.

Smith, D. S. (U.S.A.). The fine structure of central and peripheral synapses in the insect nervous system.

Wolbarsht, M. L. (U.S.A.). Wing sense organs in the flight of Diptera.

FEEDING AND NUTRITION

OBSERVATIONS ON *RHODNIUS PROLIXUS* FED ARTIFICIAL DIETS

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The development of a practical apparatus for feeding all stages of *Rhodnius prolixus* artificial diets (2) and the discovery of chemicals that would stimulate the insects to gorge on artificial diets (3) have enabled us to feed *Rhodnius* nymphs a series of artificial diets. These diets have allowed us to study the relation of abdominal distension and nutrition to moulting (1). When fourth-instar nymphs are fed on 0·15 M NaCl solution the solution moves out of the gut into the haemolymph space, collapsing the gut within 36 hours after feeding; the abdominal walls are still stretched. Under these conditions the moulting cycle is initiated. When similar nymphs are fed 0·15 M NaCl plus 6% dextran, the solution remains in the gut; therefore the gut and the abdomen are stretched. The amount of distension is similar to that in animals fed on blood. Under these conditions the moulting cycle is initiated. As there are no available nutrients in either of these diets, moulting can be initiated solely by the mechanical stimulus of abdominal distension.

A chemical diet consisting of 58 chemicals with bovine albumin as its least-defined constituent has been formulated. Up to 75% of the nymphs fed this diet moult once and are indistinguishable from blood-fed animals. When fed a second time on this diet the insects will not moult again. If fed on rabbit blood after a successful moult following the chemical diet, the insects will develop normally. The diet either lacks some essential nutrient or the, relative concentrations of some of the nutrients are wrong. A series of modifications are now under test.

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SOME OBSERVATIONS ON THE SOLID COMPONENTS OF THE GUT CONTENTS OF APHIDS

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Most work on aphid nutrition has adopted the "black box" approach: the "input" of the aphid, the phloem sap, has been at least partially characterised for some species, while the "output", the honey dew, has been analysed in detail in many cases (1). The mechanism of digestion and absorption is however little understood, and is based on inferences from the "input and output", from morphology, histology and more recently enzyme extracts from whole guts.

Since the constituents of phloem sap are soluble, small molecular weight substances with sucrose, and a number of amino acids among the major components, it has been generally assumed that the aphid gut is a vessel for the passage of soluble materials. This is however not necessarily the case. Davidson (2) reported the presence of a white crystalline substance in the stomachs of *Aphis fabae* feeding on the spindle *Euonymus*, which was absent in *fabae* feeding on bean. *A. fabae*, *Myzus persicae*, *Rhophalosiphum* sp., and *Macrosiphum euphorbiae* vary in characteristic gut volume depending on their host plant. This is most striking in aphids that have fed on members of the Chenopodiaceae. Moericke (3) has also observed this host specific response of the crop in *A. fabae* and *M. persicae.*

The increase in volume is due to the accumulation within the lumen of the crop of an opaque white granular material which is present only in minute quantities in aphids feeding on Cruciferae or Solanaceae for example.

This host specific reaction must be due either to translocated material from the sieve tubes, which is no longer soluble under the conditions of the aphid gut, or to altered synthetic activity of the gut. The latter appears to be the case.

The crop contents of *A. fabae* feeding on beet were analysed by pooling gut contents from groups of 100 aphids. The supernatant contained sucrose, glucose, fructose and melezitose, indicating the crop to be a site of synthesis of this trisaccharide which is found in the honey dew.

The solid fraction of the gut yielded glucose and fructose plus small quantities of xylose and arabinose, on short hydrolysis, and glucose and fructose alone on longer hydrolysis. A solid red pellet remained after 1 hrs. hydrolysis in 1N HCl at 100°C.

In histological preparations the material is intensely PAS positive. Starch, pectin, cellulose and acid mucopolysaccharide are absent. Some protein is present. The material appears to be a neutral mucopolysaccharide possibly in the form of a complex with protein.

It is restricted to the crop, where it is secreted by the crop epithelium as a fibrillar mass which breaks from the surface to lie free in the crop. Fragments in the crop may accumulate further laminae.

Transglucosidase activity has been reported in gut extracts of aphids (1) and it seems probable that these are involved in the synthesis of the fibrillar material, perhaps acting at sites on the microvillar surface of the crop epithelium to give the fibrillar material, and free in the lumen to produce the laminate concretions. The histology of the crop epithelium suggests that the waves of secretory activity described for *A. fabae* by Weber (4) are modified in animals feeding on chenopod hosts.

Pending the analyses of sugar beet phloem sap it is postulated that the accumulation of polysaccharide within the crop of chenopod hosts is due to the reaction of gut glucosidases with the translocated sugars which may include xylose and arabinose as well as sucrose.

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LARVAL NUTRIENT STORES, ADULT DIETS AND REPRODUCTION IN DIPTERA

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Adult dietary needs for oögenesis vary in Diptera. Many require a dietary protein and other substances before eggs are produced. In the simuliids there are various levels of autogeny and anautogeny (1, 2). However, most simuliid species require blood to develop any eggs.

Under normal rearing conditions the house fly, *Musca domestica* L., shows no or only a low level of autogeny, but recently, by feeding larvae special diets, autogeny has been increased (6). When larvae were reared on the usual CSMA medium and adults fed a diet of ten L-amino acids, sucrose, salts and water (Diet 1), eggs were produced. However, oviposition ceased after a short period while milk-fed flies continued to oviposit (5).

Yet, when individual females were fed Diet 1, supplemented with cholesterol and B-vitamins, fecundity was enhanced but slightly. Only when this diet was further supplemented with RNA (Diet 2), did repeated ovarian cycles develop (5). The improvement in fecundity was statistically significant. Third and fourth cycles were only laid with RNA in the diet. Also more flies oviposited per cycle with Diet 2, in addition to the greater individual fecundity. In contrast, the addition of RNA to the diet fed to *Drosophila* adults had little effect on fecundity (7). If adenine and cytidylic acid replaced RNA in the house-fly diet, egg production was as high or higher. Yet when the RNA was replaced by adenine alone, a poorer fecundity resulted. Presumably sufficient RNA or its precursors are available from the larval fatbody, which is autolysed in adults (3), to supply one ovarian cycle and occasionally two. Also, when the level of the amino acid, methionine, was increased in the adult diet, more eggs were laid until an asymptote was reached. However, when no methionine or cystine was present in the diet, adults laid a few eggs, implying that some methionine was also stored and transferred to the adult.

When house-fly larvae were reared axenically on a semidefined medium, developed by Monroe (1962), they grew more slowly and were smaller than CSMA-reared larvae. By changing the concentration of sodium oleate, RNA and cholesterol independently in our larval diet, each of these chemicals was shown to influence pupal weight and the number of ovarioles per ovary (8). Adult survival, and indirectly fecundity, was influenced by the amount of RNA and to a less extent by that of the oleate in the larval diet. In addition to a greater adult survival, these females fed Diet 1, laid up to four cycles of eggs, while CSMA-reared flies rarely developed more than one cycle. When our larvae were axenically reared with the cholesterol level raised to 0·5%, oögenesis was initiated in about half the sugar-fed females but did not reach completion after 14 days. Others, by raising the amount of cholesterol in the CSMA or sterile diet fed to house-fly larvae, found autogeny in over 50% of females fed on sugar-water only (6). However a 1-3% autogeny occurred in their strain of house flies when larvae were reared on non-supplemented CSMA (6). Thus the importance of the genetic effect is suggested.

Therefore, autogeny even within one species of Diptera may depend on the abundance and quality of food available to the larvae, on the amount of stored reserves, on other environmental conditions, and also on the genetic differences between strains. This genetic effect may influence the metabolic activity of the larvae or the extent to which synthesis and release of hormones occurs. Besides these physiological manifestations of autogeny, autogeny has also been followed by the evolution of behavioural and structural features (1, 2).

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THE STRUCTURE AND FUNCTION OF GONADS OF ALFALFA PLANT BUG—*ADELPHOCORIS LINEOLATUS* (GOEZE) (HETEROPTERA, MIRIDAE) AFFECTED BY FOOD

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The gonads of adults fed on flowering alfalfa were studied. Striking changes were observed in specimens fed on experimental diet.

All the stages of development of spermatic cells forming successive regions starting from the apex, were observed within the cysts of the tubules. Spermatogenesis takes place undisturbed most of the life. The overall length of tubules decreases in old specimens (24th day) due to the shrivelling of the active spermatogenetic tubular parts. The length of the basal region of empty cyst cells remains constant. The spermatocytes or spermatogonia of some cysts degenerate—their nuclei become pycnotic and gradually all the cells change into intensively basophil degenerative granules. The inner cyst framework is histolysed and the unripe germinal cells are released.

The testicular tubules of males fed on flowerless alfalfa show a sharp fall in the length already on 5th day, when also a degeneration of spermatic cells takes place. This decline is very striking when the males are starved or fed on 10% glucose solution; spermatic cells degenerate within 24 hours. These disturbances occur in males, fed on 10% honey solution, only on the 12th day and in very old specimens fed on flowerless alfalfa to which wadding soaked with honey or glucose solution or aphids were added.

The specialized trophocytes of the telotrophic ovarioles of newly emerged females release immediately a secretion which activates the oocytes and is the only source of nutrients during previtellogenesis. The prefollicular tissue around the oocytes in this period undergoes morphogenetic development into a differentiated epithelium of binucleate cells, supplying the oocyte with nutrients during vitellogenesis. The development of oocytes is serial for a great part of the life. The last but one oocyte reaches $\frac{1}{2}$ of the length of that on the lowest level. In old females (24th day) the morphogenesis of the prefollicular tissue and thus also vitellogenesis is delayed, the difference of length of these oocytes increases. Finally, vitellogenesis ceases and the oocytes at that stage are resorbed by the action of follicular epithelium.

In females fed on alfalfa deprived of flowers the delay in morphogenesis of prevalent part of ovarioles occurs on 3rd day; the disorder of vitellogeny ends by its ceasing already on 8th day when the resorption of oocytes begins. In females starved or fed on glucose solution only previtellogeny takes place. The follicular epithelium never develops and in consequence oocytes are never resorbed. Delayed morphogenesis and thus disorder in vitellogeny were observed in females fed on alfalfa deprived of flowers to which wadding soaked with glucose solution were added; resorption of oocytes was ascertained, nevertheless, only in old specimens. The disorder in vitellogenesis was observed on 12th day in females fed on honey solution and only in the very old ones fed on alfalfa deprived of flowers to which wadding soaked with honey solution or aphids were added.

A degeneration of spermatic cells as well as delayed or stopped morphogenesis of prefollicular tissue, ascertained as signs of senility of alfalfa plant bug, may be induced by feeding on food where the essential particles are absent (starvation, glucose solution) or are present in a very low concentration (vegetative parts of alfalfa). These changes result in a diminished fertility in males and stoppage of the development of oocytes at previtellogeny in females. These particles are obtained in high concentration in the nectar of flowers and in honey. It may be of a vitaminous character.

DEVELOPMENT

DETERMINISME DE LA PRODUCTION DES FORMES SEXUPARES OU SEXUEES CHEZ LES APHIDES

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Une courte photopériode entraine l'apparition des sexupares ailés (SL) ou aptères chez de nombreuses espèces d'*Aphididae.* "L'effet de groupe" combiné à une longue photopériode provoque, avec des modalités variées, l'apparition des virginipares ailés (VL) (1).

Dysaphis plantaginea Pass. constitue un cas particulier: l'effet de groupe combiné avec une longue photopériode n'occasionne pas l'apparition de VL; en revanche, il intervient dans la production des SL lorsqu'il est combiné avec une scotopériode de 16 ou de 24 h. (obscurité permanente).

Des larves au 4ème stade ou de jeunes imagos ont été récoltés dans une souche élevée sous une scotopériode de 8h. et à 20° et élevés en groupe ou isolément sous une scotopériode de 8, 12, 24h. entre le début de juin et la fin septembre.

La fig. 1 indique les délais d'apparition des SL sous diverses conditions expérimentales.

Diverses hypothèses peuvent être émises sur le mécanisme de l'apparition des SL; la plus simple est d'admettre qu'elle est liée à la secrétion d'une hormone *Hs* qui ne peut se produire que lorsqu'une autre secrétion hormonale, appelée "facteur fondatrice" (1, 2) ou "interval timer" (3, 4), ne se manifeste plus.

On peut admettre que les SL commencent à apparaître dès qu'une certaine quantité-seuil d'hormone que je désignerai par *SHs* est accumulée dans l'organisme maternel.

4 scotopériodes consécutives de 12 h. combinées à l'effet de groupe provoquent le début

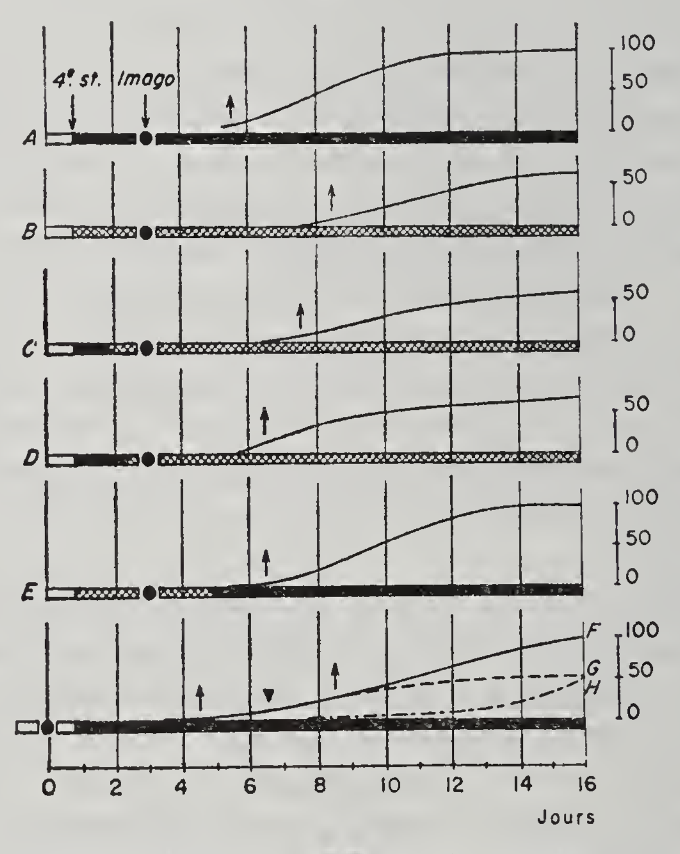

Fig. 1. Les pucerons aptères provenant d'une souche élevée sous une scotopériode de 8h. et à 20° ont été élevés à partir du 4ème stade larvaire ou du stade imaginal sous une scotopériode de 12 h. ou de 24 h. (obscurité permanente) en groupe (lots A à F) ou isolément (H); le lot G a été élevé en groupe pendant 6 jours puis isolément; en ordonnées: pourcentages de sexupares ailés.

d'apparition des SL; cela revient à dire que chaque scotopériode de 12 h. produit une quantité d'hormone de *SHs*: 4 soit 0,25 *SHs*. Les quantités d'hormone produites sont, pour les essais réalisés entre le début de juin et la fin septembre:

0,125 *SHs* pour une scotopériode de 12 h. sans effet de groupe.
0,125 *SHs* pour une scotopériode de 24 h. combinée à l'effet de groupe.
0,08 *SHs* pour une scotopériode de 24 h. sans effet de groupe.

Les secrétions hormonales produites par l'effet de groupe et une scotopériode de 12 ou de 24 h. s'additionnent (Fig. 1, lots C, D, E) et les SL apparaissent quand la somme des quantités d'hormone produites par les diverses conditions expérimentales est égale à *SHs*.

La valeur de ces coefficients hormonaux varie avec l'âge de la feuille de *Plantago lanceolata* L.; le stade de développement de la feuille conditionne également la possibilité de développement des jeunes femelles sexuées (2).

Il était intéressant de préciser la persistance chez les pucerons de l'hormone *Hs* produite par l'effet de groupe ou les scotopériodes de 12 h. La comparaison des lots F, G, et H montre que l'action de l'effet de groupe cesse à partir du 4ème jour.

Les SL cessent d'apparaître après 1 ou 2 scotopériodes de 8 h. Il semble que la scotopériode de 8 h. inhibe l'hormone *Hs* mais qu'elle ne la détruise pas. En effet, les SL apparaissent après 4 ou 5 scotopériodes de 12 h. séparées par des scotopériodes de 8 h. de façons variées.

La production des SL cesse également après 48 h. d'exposition des pucerons à une température de 24° combinée à une photopériode de 8 ou de 12 h.

La production des mâles est indépendante de l'effet de groupe; en soumettant à une scotopériode de 12 h. des pucerons à différents stades on constate que le délai minimum entre le début de l'exposition à 12 h. et l'apparition des mâles est de 18 jours pour de jeunes adultes, et de 13-14 jours pour des larves au 1er ou au 4ème stade.

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THE GENERALITY OF TEMPERATURE EFFECTS ON DEVELOPMENTAL RATE AND ON OXYGEN CONSUMPTION OF DEVELOPING INSECT EGGS

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It has been known for many years that if one plots the length of time from egg laying to hatching at various temperatures from minimal to maximal, one obtains a curve that is close to being a hyperbola. Correspondingly, the developmental rate curve is close to a straight line. The question we have studied is why should there by a sharp cut-off at the low temperature end.

Various tests have shown that there is no particular sensitive period, no block to hatching itself, and no detectable organ or histopathology for subminimal temperatures. But there is a much greater weight loss, and hence greater energy expenditure, at minimal temperatures. On Arrhenius type graphs, oxygen consumption plots a straight line whereas growth rate plots as a strongly downwards curved line. This led originally to the suggestion that the temperature threshold is the point at which the stored reserves in the egg become exhausted. But several points made this interpretation appear untenable and led to the suggestion of a metabolic upset due to varying kinetics of different physiological systems. Biochemical studies now underway lend support to the last hypothesis but the critical steps have not yet been identified.

Full data on eggs of a bug, a grasshopper, a moth, a beetle, a mosquito and the house fly are presented in *Physiological Zoology*, 1964, 37: 199-211.

STRUCTURE ET CONDITIONS DE FORMATION D'EXUVIES ÉPAISSES OBTENUES EXPERIMENTALEMENT CHEZ *BOMBYX MORI* L.

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Après certaines circonstances expérimentales, en particulier ligatures en un point variable du corps, nous avons obtenu il y a longtemps (1) des chenilles formant à la mue nymphale une exuvie d'épaisseur anormale soulevée par un abondant liquide sous-jacent; dans lequel Amanieu et Jeuniaux (2) ont prouvé par des techniques fines et élégantes, la présence de chitinase.

Si l'on compare le tégument d'une nymphe normale en exuviation et celui de la portion de nymphe amputée issue d'un ver ligaturé, on observe par les techniques histologiques classiques (R. Ratel (3)):

1° — que l'épiderme des opérés ressemble à celui d'une prénymphe normale et non à celui d'une nymphe (lequel a un aspect en colonnade)

2° — que la nouvelle cuticule formée est à peu près normale

3° — que la cuticule ancienne soulevée comprend toutes les couches d'une cuticule complète n'ayant pas subi la résorption de l'endocuticule profonde.

Les images électroniques confirment cette anomalie et, en plus, montrent que les strates parallèles endocuticulaires sont séparés par des espaces vides d'épaisseur équivalente traversés par des ponts reliant les strates persistants (4).

Etant donné que cette anomalie a été obtenue à la suite de sections du système nerveux, de destruction de ganglions, (1) la cause initiale doit être la lésion du système nerveux provoquée par la ligature.

Diverses observations et expériences permettent d'envisager sa génèse: d'abord la découverte que le liquide abondant sous-cuticulaire était pour une bonne part formé de sang (5).

La présence de ce sang est déterminante car en provoquant, comme nous venons de le réaliser, un afflux de sang dans l'intestin grâce à l'injection dans le tube digestif de solutions hypertoniques, le volume de liquide sous cuticulaire diminue ou reste normal et l'exuvie est beaucoup plus mince.

Ce sang manifestement, dilue la sécrétion, riche en enzymes, de glande d'exuviation. Cependant l'attaque de certains strates seulement, suggère que ce sang n'agit pas uniquement par dilution mais en genant our empêchant spécialement certaines réactions.

L'injection de protéase, sous l'exuvie en formation, a provoqué, en 2 jours, la formation d'une exuvie mince (et non épaisse comme chez les sujets ligaturés non traités).

Le sang gênerait donc l'action protéolytique du liquide exuvial.

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INFLUENCE D'UN INHIBITEUR DE L'ACIDE FOLIQUE SUR L'OVOGENESE DE LA DROSOPHILE

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Chez la Drosophile, le rôle de l'acide folique peut être analysé en incorporant un inhibiteur spécifique au milieu nutritif. Le blocage de la vitamine par l'aminoptérine détermine d'importantes modifications de l'ovogénèse qui seront exposées ici.

Etude des caracteristiques de la ponte (1)

Administrée aux adultes, l'aminoptérine détermine essentiellement une réduction de la taille des oeufs et de la longueur de leurs filaments, une diminution du nombre d'oeufs pondus et du pourcentage d'éclosion. Ces modifications sont proportionnelles à la concentration et on aboutit généralement à une stérilité complète après trois ou quatre jours, dès que la nourriture contient plus de 0,5 p. p. m.

L'acide folique, ajouté en excès et en même temps que l'aminoptérine, supprime les effets toxiques.

L'arrêt de l'intoxication des femelles stérilisées permet habituellement une restauration à peu près complète des caractéristiques de la ponte. Cependant, la récupération est d'autant plus lente que la dose toxique était plus forte ou que le traitement a été plus long. En outre, un excès d'acide folique dans le milieu n'accélère pas le processus de restauration.

Modifications cytologiques de l'ovogénèse chez les femelles stérilisées

Après deux ou trois jours d'intoxication, on observe une dégénérescence des follicules ovariens aù moment où commence le dépot de vitellus dans l'ovocyte. Les étapes de cette dégénérescence semblent les suivantes:

(1°) les noyaux des cellules nourricières prennent un aspect anormal;

(2°) la plupart des noyaux nourriciers disparaissent; cependant quelques uns persistent habituellement, grossissent et demeurent bien colorables.

(3°) les cellules folliculaires disparaissent sauf quelques unes qui s'aplatissent considérablement.

Parvenue à ce stade, la résorption s'arrête et les cellules qui persistent gardent le même aspect pendant plusieurs jours. Ces cystes dégénérés s'entassent à l'extrémité des ovarioles et sont parfois évacués à l'extérieur.

Lorsque la concentration d'aminoptérine est forte, la production des cystes nouveaux se ralentit progressivement et on observe souvent des fusions entre cystes adjacents. Après une dizaine de jours, la formation de nouveaux cystes est complètement arrêtée mais les cellules de la zone germinative continuent à se diviser et à grossir de sorte que le germarium de chaque ovariole se renfle beaucoup et prend un aspect tumoral.

Si la concentration d'aminoptérine est plus faible, la formation de nouveaux cystes n'est pas interrompue mais leur croissance parait ralentie. Dans ces conditions, le nombre des cystes en train de croître dans chaque ovariole augmente et peut atteindre une dizaine. Arrivés à une certaine taille, ces cystes dégénèrent et s'entassent dans la partie inférieure de l'ovariole.

En conclusion, les effets de l'aminoptérine sur l'ovogénèse sont très progressifs et dépendent à la fois de la dose et de la durée de l'intoxication. D'après les observations cytologiques, l'aminoptérine semble inhiber surtout la croissance des noyaux nourriciers et la formation des cystes. Il est intéressant de souligner qu'une dose élevée de toxique, qui arrête la ponte en trois jours, est incapable d'arrêter complètement les divisions cellulaires deux semaines après le début de l'intoxication.

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THE EFFECTS OF X-RAYS ON THE MEAL WORM, *TENEBRIO MOLITOR*, EMBRYO

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The present study reports the findings pertaining to the proteins and the free amino acids found in the developing meal worm embryo, the variations observed following X-ray stimulation, and the preparation of survival curves for the X-irradiated embryo.

Data for the meal worm embryo shows that its resistance to X-irradiation increases with each day of embryological growth. The dosages required to yield a 50/8 M.L.D. effect ranged from 150 r for the one day old embryo to 41,000 r for the eight day old embryo. The survival curves obtained for this period of development indicate that resistance to irradiation builds up rapidly to the fourth day of growth. After that interval the resistance increases at a slower rate.

The a-amino N content, free amino acids and derivatives, detected in the developing embryo also showed a progressive increase in concentration during this period of growth. A total of 20 free ninhydrin positive compounds have been identified on one and two-dimensional paper chromatograms for the normal embryo. There was a general increase in concentration for these compounds during the course of embryological development.

Paper electrophoretic patterns of the proteins found in normally developing embryos are represented by two distinct anodal fractions separated by an area of low concentration.

The effects of X-irradiation on the embryo are characterized by a third and fast moving anodal fraction. When this occurred in the older embryos, 4 to 6 days old, the induced fraction gradually subsided and disappeared in about 72 hours. These embryos successfully completed their embryological growth.

During this same period there was a disturbance in the amino acid "pool" in that asparagine, arginine, histidine, phenylalanine, serine, threonine, tryptophane, tyrosine and valine increased in concentration while a-alanine, aspartic acid, cystine, glutamic acid, glutamine, glycine, methionine and proline decreased in concentration in comparison with normal values. These variations were gradually readjusted to normal conditions by the surviving embryos during the post-irradiation period.

Although other factors are to be considered with respect to this response to X-rays, the approach to the problem through amino acid reactions seems feasible. As amino acids provide some protective action, a part of the radiation resistance of insects may be explained by means of this physiological factor.

THE FINE STRUCTURE OF SOME TISSUES OF *RHODNIUS PROLIXUS* DURING MOULTING

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Insects in the fifth instar were fed blood and allowed to begin moulting. At one day intervals, samples of the epidermis, alar muscles, the pericardial cells, the blood cells and fat body were observed with the E.M.

The epidermis in a fasting animal is thin, with shrunken nuclei. The mitochondria also are shrunken. The endoplasmic reticulum (E.R.) is well formed with many loops and concentric balls of ribosomes lining double membranes; there are no cisternae. There are many loose ribosomes. No smooth E.R. is seen. No glycogen is apparent; but there are many pigment granules in the cytoplasm. Where two cells come together the cell membranes form many interdigitations and show large and small septate desmosomes and loose juxtaposition.

By the third day the epidermis is considerably thickened. The nuclei and nucleoli are enlarged and the rough E.R. has many cisternae. Some very elongate mitochondria are seen. There is as yet no extensive glycogen storage in the cytoplasm but many dark staining lipid-like granules appear in addition to the many layered pigment granules. The lipid-like granules are often seen associated with a smooth E.R. Golgi complex.

By mid-moult the epidermis is at its thickest. The rough E.R. is mostly cisternae; there are many empty vacuoles as well as dark staining granules. The mitochondria are turgid short rods, only occasionally elongate. The beginnings of a new cuticle is laid on the outer surface of the epidermal cells. This outer surface has many microvilli attached to the new cuticle. Glycogen stores are commonly seen in the cytoplasm.

By the end of moulting a gradual thinning of the cells occurs. There is still much smooth and rough E.R. At the cuticular surface of the epidermis, there are many irregular microvilli. There are many lipid-like and pigment granules in the cytoplasm. Glycogen is rarely seen.

The fat body in a fasting animal is a thin sheet of cells with dense, often shrunken, mitochondria. The nuclei are commonly indented, and the nucleoli are small. The many ribosomes are loose in the cytoplasm. Many dark staining lipid-like bodies are seen. These resemble lysosomes. Some have internal membrane bounded substructures. There are no pigment granules; there is no stored glycogen. There are however, a few large empty vacuoles. Fat cells have a loose union of their cell membranes; there are no desmosomes, although microvillus interdigitation is seen.

As moulting progresses each fat body cell and its nucleus and nucleolus increases to many times its fasting size. Large vacuoles appear and a great deal of glycogen is seen. The mitochondria are large and turgid and show evidence of division. The size of the mitochondria is three to four times that of epidermal cells.

In mid-moult the mitochondria become very dense with continued evidence of division. The E.R. is mainly cisternae.

Just after moulting the mitochondria are less dense again; stored glycogen is abundant as are the large vacuoles. Many of the dark staining bodies are still present. The rough E.R. continues to be well formed.

After a period of fasting the glycogen granules disappear, the mitochondria and nuclei shrink, the E.R. disorganises leaving the ribosomes loose. The dark staining lipid granules or lysosomes become very obvious.

DIAPAUSE OF MATERNAL ORIGIN

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The environmental factors responsible for the induction of facultative diapause in insects are most commonly photoperiod and temperature (3). The "sensitive stage" and the resulting diapause, although often separated by several intervening instars, usually both occur during the life of a particular insect. The parasitic wasp, *Nasonia vitripennis*, however, is one of several examples now known in which the sensitive stage and the diapause occur in successive generations.

Chronological analysis of the offspring of two strains of *Nasonia vitripennis* kept in a variety of environmental conditions has produced the following results. Females kept in continual darkness at 25°C. and supplied with two pupae of *Sarcophaga barbata* daily, produce a few diapause larvae at the beginning of reproductive life but change to the production of developing progeny after the first few days. Females of one strain (C strain, isolated in Cambridge) then switch to the production of diapause larvae again later in life so that a distinct age-pattern is seen (2). The females of the other strain (WH+, the Woods Hole "wild type") do not show such a pattern in these conditions. Virgin and fertilised C strain females produce diapause larvae in exactly the same manner, and crossing experiments between the two strains indicate that, although the diapause-characteristics of the strain are under ultimate genetic control, the mechanism of diapause induction is purely maternal and the males play no part in determining the development of their immediate progeny. The way in which females change from the production of one type of larva to the other resembles the "maternal switch" mechanism described by Lees (1) for the aphid *Megoura viciae*.

Lowering the temperature at which the adult females are kept results in a lower daily egg production and an extended reproductive period. The age at which the "maternal switch" operates, however, is not materially altered, so that a much greater proportion of the progeny are produced as diapause larvae. Females of the WH+ strain also switch to diapause larvae at 20 and 15°C, presumably because of the extended reproductive period.

The most important factor inducing diapause in *Nasonia* is photoperiod, again operating through the maternal generation. Short daylength causes the females of both strains to switch to the production of diapause larvae earlier in life and long daylength prevents the appearence of diapause. Continual darkness, as described above, has an "intermediate" effect. Changing the females from low to high temperatures, or from short to long daylength during the reproductive period, causes the appropriate switch from diapause to developing larvae after an initial time lag.

Nasonia vitripennis behaves as a typical "long-day" insect in response to photoperiod, and the state of diapause in the fourth instar larva appears to be of the normal larval-pupal type involving inactivation of the brain-prothoracic gland system. However, since the sensitive stage and the resulting diapause occur in successive generations the mechanism of diapause induction cannot operate solely through the mediation of the central nervous system and a chemical "factor" must be postulated which is passed from the parent female through the egg to the larva.

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AESTIVATION: ITS OCCURRENCE IN INSECTS

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This paper will summarise briefly the recorded accounts of aestivation in insects: its occurrence, environmental stimuli, and physiological consequences.

Aestivation, *per se*, has been recorded in at least thirty-seven insect species representing five major orders (Table). Although aestivation appears principally in the adult stage, literature shows this phenomenon to occur in the other life cycle stages for some insects. Most examples of aestivation occur in arid and semi-arid regions, and in several cases, when a species (Ex: *Hylemyia antiqua* and *Phyllopertha nazarena*) extends over a considerable latitude, hibernation may occur in northern areas while aestivation is found in the south.

Lees (1, 2) and de Wilde (5) have discussed the environmental factors: light, temperature, humidity and nutrition, as they influence the onset of diapause. In the context of these three articles, the aestivating insects which are photoperiod-dependent would be classed as "short-day" insects with diapause occurring in the long days of summer. However, most aestivation literature presents scant specific evidence concerning the influence of environment; instead, most writers imply that elevated temperatures alone or in combination with lengthening photoperiod, decreased humidity, or loss of food act as causative agents. Whatever the external causes might be, the stimuli must still be transduced into an endocrine change which then produces diapause manifestations of physiological and biochemical character.

It has been assumed that the physiological alterations would mirror those of hibernation; and except for one paper, this had not been checked until recently. Pepper (3) reported that a low catalase level corresponded to the period of adult aestivation in the army cutworm. During adult aestivation of the weevil *Hypera postica*, *in vivo* respiration decreased 82%, fat increased from 3 to 15% and water decreased from 70 to 55% (4). These data compare favourably with results of others concerning the physiological alterations of insects during hibernation.

Table

Five orders, thirteen families known to contain aestivating insects

Orders	*Families*	*Representative Insects*
Coleoptera	Coccinellidae	*Coccinella septempunctata*
	Curculionidae	*Hypera postica*
	Scarabaeidae	*Phyllopertha nazarena*
Diptera	Anthomyiidae	*Hylemyia brassicae*
	Culicidae	*Aedes squamiger*
Homoptera	Psyllidae	*Psylla pyri*
	Aphidae	*Periphyllus lyropictus*
Hymenoptera	Formicidae	*Pogonomyrmex occidentalis*
Lepidoptera	Bombycidae	*Bombyx mori*
	Geometridae	*Abraxas miranda*
	Noctuidae	*Chorizagrotis auxiliarus*
	Noctuidae	*Barathra brassicae*
	Scythridae	*Syringopais temperatella*

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PHYSIOLOGY AND BIOCHEMISTRY OF INSECT FLIGHT

PHYSIOLOGICAL AND MORPHOLOGICAL CHANGES IN THE FLIGHT MUSCLE OF THE AGING HOUSE FLY *MUSCA DOMESTICA* L.

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During the course of an extensive study on the biochemical basis of aging in the common house fly, it was recorded that the male has an average life span of about 17 days and the female about 29 days. Correspondingly, the male loses its ability to fly much earlier in life than the female, as a result of the abrasion and ultimate loss of the wings, which begins at 5 to 6 days after emergence in the male, and during the third week after emergence in the female. These physical manifestations of aging are found to be concomitant with the decline in the activity of mitochondrial Mg-activated adenosine triphosphatase (ATPase). ATPase activity increases during the first 5 to 6 days after emergence in the male by about 65% and then decreases during the next 6 days to a minimum level. Concomitantly the content of adenosine triphosphate (ATP) (substrate for ATPase) in the thorax rises significantly after the first week and reaches a maximum value by the 9th day, i.e., the period when the enzyme system involved in dephosphorylation of ATP is at its minimum. Unfortunately the coincidence of wing loss and decline in ATPase activity, at virtually the same time, gives no firm idea as to cause-and-effect relationship.

On the other hand, the observed decline in the activity of cytochrome *c* oxidase about 4 days *after* the onset of wing loss, suggests that the activity of this enzyme may be associated with the internal structural changes *resulting* from the wing loss.

Studies on another important enzyme system, alpha-glycerophosphate dehydrogenase (GDH), involved in intermediate metabolism of carbohydrates and, therefore, important in energising flight, indicate that the decline in its activity precedes the loss of wings by about 48 hours. This strongly suggests that GDH loss may be a chemical forerunner of senescence of flight ability.

Although experimental de-alation has neither an effect on the longevity of the flies nor upon the activity of mitochondrial ATPase, it results in the persistence of GDH activity at the peak level (4 days) throughout the life span of the de-alated fly. This suggests that the originally intact wings of young flies are themselves indirectly responsible through a negative feedback mechanism, for the ultimate failure of certain biochemical elements, and ultimately, therefore, for the actual failure of flight ability, in the loss of wings themselves.

In order to determine more closely the relationship between wing loss and related biochemical changes, studies were undertaken on the distribution of mitochondria, which are regarded to be the chief, if not the exclusive sites of most of the enzymes involved in the aerobic phases energising flight. It has been observed that the loss of wings preceded the loss in number and size of giant mitochondria of the flight muscle of the house fly.

This clearly points to a genetically programmed time-dependent factor for longevity and failure of ATPase, both of which are independent of the presence of wings and associated structural and biochemical changes.

THE FUNCTIONAL ORGANISATION OF THE FLIGHT SYSTEM IN BELOSTOMATID BUGS (HETEROPTERA)

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The Belostomatidae include the largest insects whose main flight muscles are known to be of the fibrillar, asynchronous type. We have studied flight mechanisms in five species of this family: *Lethocerus maximus*, *L. uhleri*, *L.* (*Benacus*) *griseus*, *L. cordofanus* and *Hydrocyrius columbiae*. The work has concentrated on the mesothorax because the fibrillar flight muscles, and most of the accessory ones, are located there. The metathorax has a well developed pair of wings but their use in flight appears to be wholly dependent on being mechanically coupled to the forewings.

There are four pairs of fibrillar muscles in the mesothorax. The dorsal longitudinal muscles provide power for the downstroke and, at the same time, automatic pronation of the wings. The dorsoventral muscles provide upstroke power and automatic supination during that stroke. The oblique dorsal muscles act mainly as wing supinators so that their function during flight is largely one of control. The fourth pair of fibrillar flight muscles are basalars which act indirectly via an insertion on the pre-episterna. Their action is that of an accessory wing depressor and pronator. Since the oblique dorsal muscles probably act antagonistically to the basalars during flight it must be assumed that they are both effective during wing downstroke.

The only direct flight muscles in the mesothorax are the tonic wing folding muscles which insert on the third axillary sclerites. Two pairs of tergo-coxal and one pair of tergo-trochanteral muscles help keep the legs in flight position and may also act as tonic wing elevators. The function in flight of other thoracic muscles which insert on the leg is not known. Several pairs of short, accessory, indirect muscles strengthen the thoracic framework but their function in flight is also unknown.

The pterothorax contains a fused meso- and metathoracic ganglion. The most anterior nerve trunk from this ganglion provides the motor supply to the dorsal longitudinal and oblique dorsal muscles. It also supplies the prothoracic retractor muscle which inserts in the mesothorax but otherwise innervates no other mesothoracic muscles. There are no recurrent nerves between pro and pterothoracic ganglia yet some of the motor neurons of the dorsal longitudinal and oblique dorsal muscles are located anterior to the pterothoracic ganglion. This is not true of the motor neurons of any of the other pterothoracic muscles. There are at least three motor units in each oblique dorsal muscle and five or more in each dorsal longitudinal muscle. The motor neurons to these muscles show a conduction velocity of 2·5-2·7 meters/sec at 25-26°C.

The anterior nerve trunk of the pterothoracic ganglion also supplies a sensory nerve to the wings, a small nerve which supplies the mesothoracic scolopophorous organ as well as sensilla of the lateral and ventral body wall, and a sensory nerve which innervates mechanoreceptors of the mesotergum. Both dorsal and ventral body wall sensilla are very sensitive to either air borne or water borne vibrational stimuli. The role of none of these sense organs in flight is known. The second nerve trunk of the pterothoracic ganglion supplies all of the other mesothoracic muscles as well as one nerve to the mesothoracic legs.

We have observed four species of Belostomatidae in flight: *Lethocerus maximus*, *L. uhleri*, *L. griseus* and *Hydrocyrius columbiae*. Wing beat frequency for a specimen of *L. maximus* 105 mm. long and weighing 23·4 g. was 21-25/sec at 23-24°C. For *Hydrocyrius* 57 mm. long and weighing 2·9 g. wing beat was 30/sec. For *L. uhleri* typical values are 42 mm. long, 1·7 g. weight and a wing beat frequency of 38/sec. We have also been able to record electrical activity in the four fibrillar muscles and the three tergal leg muscles during wing opening and/or tethered flight.

The three fibrillar muscles from which recordings were made during wing opening (dorsal longitudinal, oblique dorsal and dorso-ventral muscles) all display strong spike activity coincident with wing opening. The wings may be held open indefinitely without flight and when this happens the fibrillar muscle activity subsides to a lower level within a few seconds.

When the wings are held open in the absence of wind the electrical activity may cease. Once open, the wings may be held open in the absence of any muscle tension. This is probably due to a mechanical click mechanism between the third axillary sclerite and two small projections from the underside of the wing.

When flight is initiated directly from closed wings a phasic burst of spikes is recorded initially from the three pairs of fibrillar muscles but this subsides quickly to a lower level characteristic of steady flight. However, when flight is initiated from open wings these muscles are already active electrically and there is no change in pattern of spike activity signalling start of flight. Also, in steady flight it is clear that the pattern of spike activity is an irregular one and bears no temporal relationship to the regular wing beat. In the dorsal longitudinal muscles a ratio of 6 : 1 wing beats to spike frequency per motor unit has been measured. When the activity of motor units from each muscle of a pair, or from different fibrillar muscles, are recorded simultaneously it is clear that the temporal relationships among these units is also a random one.

Of the three tergal leg muscles from which recordings were made during flight only one, the coxal remoter, appears to be active. The other two, a coxal promoter and a trochanteral muscle, display activity that accounts for the distinctive flight position of those leg segments, but none peculiar to flight.

The fact that the fibrillar muscles can be electrically active with the wings open but in the absence of flight and that this activity does not change as the animal goes into and maintains flight, strongly suggests a flight initiating device similar to the "click" mechanism known in Diptera. It must be assumed that a condition of the thorax which allows oscillatory contractions of the fibrillar muscles is brought about by the action of one or more pairs of tonic accessory muscles. The muscles involved in this action and the precise thoracic changes necessary remain to be elucidated.

ELASTICITY AND WING MOVEMENTS IN INSECTS

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The principle of a mechanical oscillator is that the kinetic energy of the moving member is stored as elastic energy and released as kinetic energy when the movement reverses. It has been known for some time that the locust thorax has elastic properties reminiscent of this although very different from a simple harmonic oscillator (2). This system has now been analysed further, partly from the point of view of power consumption and partly by a more direct approach.

When the lift of a flying locust increases, the wing stroke frequency also goes up so that the increase in metabolic rate could be due both to the increased aerodynamic work and to an increase in the work done against wing inertia. However, simultaneous measurements of metabolic rate, lift and wingstroke parameters showed that the inertia term could account only for $\frac{1}{4}$ of the energy expenditure (4) in spite of the fact that the work against mass forces is of the same order of magnitude as the aerodynamic work (Weis-Fogh (3), and unpublished). Consequently, an elastic system must absorb and release energy and so reduce the work necessary for oscillating the wings.

The direct analysis showed that the locust thorax (*Schistocerca gregaria*) is in fact elastic and so strong that it can account for the acceleration during the downstroke due to the release of elastic energy stored during the upstroke. Moreover, the following figures show that the elastic efficiency is high and, also, that the elasticity resides in three different structures: intact thorax $0{\cdot}86 \pm 0{\cdot}02$; empty box $0{\cdot}88 \pm 0{\cdot}02$; elastic hinges $0{\cdot}97 \pm 0{\cdot}02$; non-active muscle $0{\cdot}8 \pm 0{\cdot}2$. One third of the energy is stored in the passive-elastic system of the wing muscles with an elastic efficiency of $0{\cdot}78 \pm 0{\cdot}16$. These figures relate to the usual speed of shortening in the flying animal and are the first direct estimates of the efficiency and of the importance of the passive-elastic component in insect wing muscle. One fourth of the energy

is stored in the resilin-containing ligaments and released with an efficiency of not less than 0·97, while the remainder is stored in and released from the hard cuticular components.

Two other migrating insects were also investigated and found to behave in a similar manner, although the details differ much. In *Aeshna* the elastic torque is caused mainly by the wing muscles and less than 25% by the thoracic box and the wing hinges. In *Sphinx* the main elastic structure is the hard cuticular box while the elastic ligaments are small or absent. Whatever the details, Table 1 shows that the presence of an effective elastic system must be universal in insects. The first column shows the calculated maximum inertia torque Q_i per unit weight and it is seen that the figures are of almost the same magnitude in the different insects. If this torque was not counteracted by elastic forces, only the muscles could provide the work for oscillating the wings and, due to differences in wingstroke frequency, this would result in a relative mechanical power expenditure represented by the last column, i.e. the wasp should use 10-20 times more power than the locust or the dragonfly merely to oscillate its wings without doing any aerodynamic work, in spite of the fact that the metabolic rate of the three insects is of the same magnitude during flight.

We can then conclude that flying insects from widely different groups possess an effective elastic system which counteracts the adverse effect of wing inertia and reduces the energy account mainly to cover aerodynamic expenses. The next question concerns the guiding principles in the mechanical design. It is already clear that different elastic structures are involved and used in different ways (muscle, solid and rubber-like cuticle) but it has also become clear that there are at least two different types of pterothorax constructed according to the same fundamental plan, one in which the tergum is suspended elastically and moves mainly up and down (locusts, dragonflies, cockroaches, beetles) and one in which the tergum is firmly supported in front and behind and in which arching and de-arching is the main type of deformation (the classical type of Snodgrass, Hymenoptera, Diptera and, maybe, Lepidoptera).

TABLE 1

Relative importance of inertia term in various insects

	Inertia figure (*gcm/g*)	*Power figure*** (*gcm/g/s*)
Desert locust*	2·5	45
Large dragonfly*	3·4	100
Cockchafer	2·1	130
Hawk moth	3·6	270
(Butterfly	0·3	2)
Bumble-bee	2·1	315
Horse fly*	2·6	470
Wasp*	5·2	755

*Metabolic rate 75-100 cal/g/h.

**This figure is proportional to the power necessary for oscillating the wing mass at the given frequency.

TABLE 2.

The influence of a linear dimension l on the wingstroke frequency n, on the inertia torque Q_i, and on the fibre stress s

Case	*Frequency*	*Inertia torque*	*Fibre stress*
(1)	$n \propto l^{-\frac{1}{2}}$	$Q_i \propto l^4$	$s \propto l^1$
(2)	$n \propto l^{-2/3}$	$Q_i \propto l^{11/3}$	$s \propto l^{2/3}$
(3)	$n \propto l^{-1}$	$Q_i \propto l^3$	$s \propto l^0$

Case (1) is calculated on the assumption that in similarly shaped hovering animals the wings produce the same amount of lift L per unit body weight ($L \propto n^2 l^4$).

Case (2) is calculated on the assumption that the ratio between the necessary aerodynamic power P_a of a hovering animal and the weight of the wing muscles is constant ($P_a \propto n^3 l^5$).

Case (3) corresponds to empirical findings in insects and birds and, moreover, is also calculated on the assumption that the fibre stress due to wing inertia is independent of size.

A less obvious guiding principle concerns the empirical relationship $n \propto l^{-1}$, (see 1). In Table 2, I have calculated the expected variations for three different cases, as indicated. It appears that the aerodynamic cases (1) and (2) have *not* been favoured by evolution. It is therefore suggested that the limiting factor has been the mattrial stresses due to wing inertia. If, namely, n is inversely proportional to l, $Q_i \propto l^3$ and the fibre stress $s = zM/I$ becomes independent of size (z is the distance from the neutral axis, M is the bending moment, and I is the moment of inertia of the cross sectional area of a bent beam). It is the strength of the elastic materials which have become the limiting factor in most cases.

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ASPECTS OF FLIGHT AT LOW REYNOLDS NUMBER

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It is generally acknowledged that the problems encountered by small insects in flying differ significantly from those met by larger insects, birds, and bats (1 and 2). Weis-Fogh and Jensen (3) have carefully documented the dynamics of flight in the desert locust, but as yet little similar work has been done on any smaller species.

Low speed and small size are complementary factors: the Reynolds number, the relevant index to the flow regime, involves a product of length and velocity. Since on both accounts small insects differ drastically from "conventional" aircraft, they fly in an exceedingly unconventional realm. As a compromise between small size and convenience, I have been using *Drosophila virilis* as experimental material. Its Reynolds number, based on wing chord and wingbeat frequency or body length and flight speed, is about 100. The comments here apply primarily to this dimensional range.

Flow at this low Reynolds number can be characterised as follows: true turbulence is absent, but separation and well defined vortices occur. Due in part to the non-statistical nature of these vortices compared with real turbulence, normally smooth plots may show odd bumps. The effects of viscosity are great: bodies experience relatively high drag forces, attributable mainly to skin friction, and trail wide low velocity regions behind. Fluid carried along with a body may act as an appreciable increment to body mass.

In addition to the normal drag problem of any aircraft, small insects such as fruit-flies have a further difficulty: propeller thrust, in order to be effective, must not be dissipated against the fuselage; however, with short wings thrust is generated quite close to the body proper. Thus a low drag body form should be an important asset even during hovering.

Drag minimization for the wings themselves is expected for several reasons. Lower drag results in improved energetic efficiency and, if associated with less displaced air, gives a lower apparent wing mass. For an oscillating wing any such inertial decrease should permit higher operating frequencies. Normally a wing experiences an increasing induced drag as the angle of attack is raised to produce lift. At low Reynolds numbers a phenomenon of opposite sign is superimposed on this: the region of low momentum flux behind the wing is wide and becomes wider with increasing angles of attack. This decrease in wake momentum flux leaves less available to be deflected. Lift and drag are then, to an extent, antagonistic.

An airplane or locust wing meets little resistance at a zero degree angle of attack, but the induced drag increases rapidly as lift is developed. The airfoil in the fruit-fly range, however, encounters a high drag at zero degrees but a proportionately lower increase as the angle becomes greater. As a consequence, instead of realising the maximum lift to drag ratio at a low angle, small insects should achieve their optimum angle of attack at or near the angle of maximum lift—the stall point. They should, then, be helped greatly by any devices which postpone stall to higher angles. For untwisted, beating wings velocity and angle of attack are greatest near the wing tip; both of these favour stalling. Thus any stall-opposing devices should be especially useful on the distal portions of the wing.

For neither of these problems—drag reduction and stall prevention—does the aerodynamic literature provide any indication of the types of devices which might be useful. At the same time an inspection of any small insect discloses an embarrassingly large number of structures whose general functions and roles (if any)in flight are unclear. For these reasons equipment for an experimental study of flight in small insects has been developed.

Measurement of the forces acting on a body moving with respect to its surrounding fluid provides the basic information on the behaviour of the body as an airfoil. For large bodies and high speeds direct force measurement is generally convenient; in the present case the requisite accuracy of a fraction of a dyne makes an indirect system preferable. A small thermistor (0·125 mm. diameter) heated to about 100°C. in a Wheatstone bridge functions as a very sensitive microanemometer for velocity mapping. Integrating a velocity map over a plane cross-section of the wake of a test object provides a measure of the momentum change of the airstream in crossing the object and hence measures drag or thrust. Since a large number of point velocity data are needed for a good map, I speed the procedure by using a motorised specimen drive and a potentiometric recorder to get continuous measurements in successive traverses of the wake. Addition of a fine wire (0·075 mm.) between airfoil and thermistor permits lift measurements also: adjustment of the fine wire by means of a micrometer to give a velocity minimum centers the wake of the wire on the thermistor and thus determines the local flow direction. Integrating a series of such data across the wake of the airfoil establishes the creation rate of vertical momentum (lift). The air stream is provided by a small, but otherwise conventional, wind tunnel constructed of 76 mm. stove pipe.

For many experiments it is useful to make photographic records of flow patterns. Again the usual techniques are cumbersome for this dimensional range. Providing the Reynolds number is held constant, shifting to a liquid system for model studies does not alter the flow patterns and allows small particles to be kept in suspension easily. The following protocol produces useful photographs with a minimum of complication: Coloured polyhexyl-methacrylate-glycolmethacrylate particles, about 0·2 to 0·5 mm. in diameter, are suspended in a revolving plexiglas bowl of liquid (brine or glycerin-water). The model is supported submerged in the liquid, its size and the bowl rotation rate adjusted to give the desired Reynolds number. Light from a mechanical or electronic stroboscope passes through a slit perpendicular to the camera axis and parallel to the flow direction; thus light strikes particles while they pass along a plane which crosses the model. Use of a stroboscope gives a dotted line for the path of each particle, so both speed and direction of flow at all points around the model are indicated in the photographs.

Work currently in progress using these techniques is providing evidence for the speculations above. The basic problem of interpreting the external morphology of small insects in terms of flight function, while exceedingly complex, now appears experimentally tractable.

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CONTROL OF FOREWING TWISTING BY HINDWING RECEPTORS IN FLYING LOCUSTS

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Mechanisms for nervous control of wing twisting in flying locusts have been investigated applying both electrophysiological and behavioural techniques. The experimental approach is based upon the lift-control reaction (1 and 3) which implies that, during steady-state flight, imposed changes in body-angle are met by adjustments of forewing twisting. Additional results have been obtained from the study of stabilisation in free flight. It appeared that two different types of control mechanisms are involved, a slow and a fast.

Control of wing twisting associated with constant lift is abolished by cauterisation of the campaniform sensilla of the wings (1). These sensilla are located on the lower surface of the subcostal vein in both pairs of wing and arranged within one hindwing group and two forewing groups of different orientation. Selective cauterisation of the group in the hindwings proved to be as effective as cauterisation of all groups. The results are shown in Fig. 1, which only relates to steadily flying animals. Frequency maxima of intact and operated animals are clearly separated (lower histogram), whereas selective destruction of the two groups in the forewings did not necessarily interfere with regulation of forewing twisting, as the dispersion

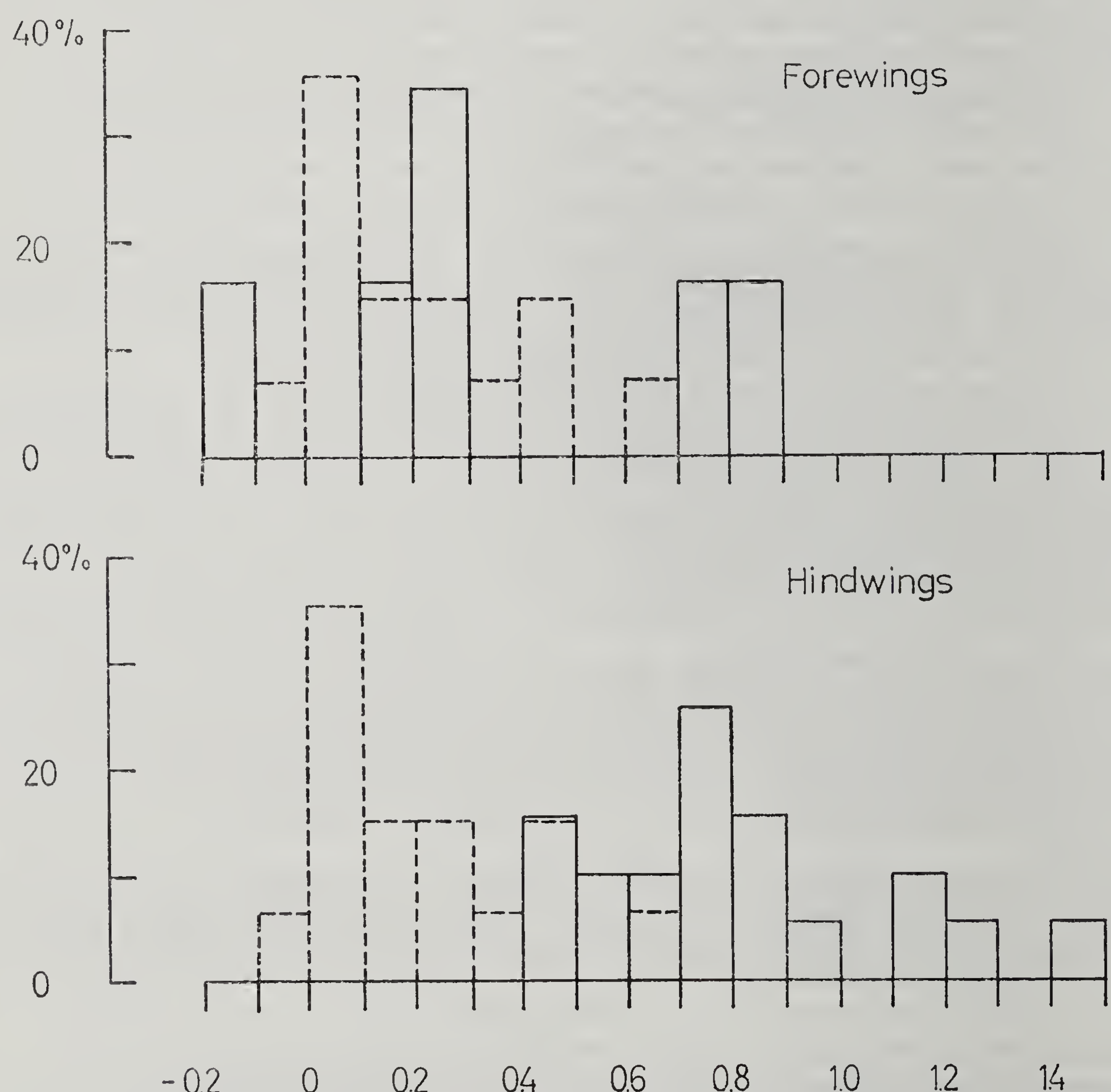

Fig. 1. Histograms summarising results of selective cauterisation applied to campaniform sensilla of the wings. Ratio of angular change of a distal wing chord to a 15° change in body-angle is displayed along the abscissa, the low values represent presence and the high values absence of control. The statistical frequency is ordinate. Samples from intact (broken line) and operated (continuous line) locusts.

along the abscissa probably originates from the interference with the feed-back routes of the motor system (upper histogram).

The slow reaction associated with constant lift permitted a further analytical approach. The relative importance of the different phases of the afferent discharge was determined by the cyclic application (at flight frequency) of an anodic block to the hindwing groups. Results can be seen in fig. 2. A block amounting to one sixth of the flight period was moved around within the wingstroke cycle. Adjustment of forewing twisting after a change in body angle of 15° depends upon the phasing of the anodic block, and is abolished when the afferent activity during the middle part of the downstroke is removed. Also, this is the period in which the lift reaches its maximum. When the discharge is suddenly abolished, the change of wing twisting builds up slowly, being completed within 100-150 wingstrokes. Furthermore, the afferent discharge from the hindwings changes with body-angle, both with respect to quantity and pattern. Natural and blocked inputs evoking same motor pattern are not equal with respect to number of firings indicating that input specifications additional to quantity are required.

It has been demonstrated that the campaniform sensilla participate in active stabilisation during free flight. In contrast to the constant-lift reaction, these control reactions occur almost instantaneously. Cauterisation of hindwing sensilla is still compatible with stable

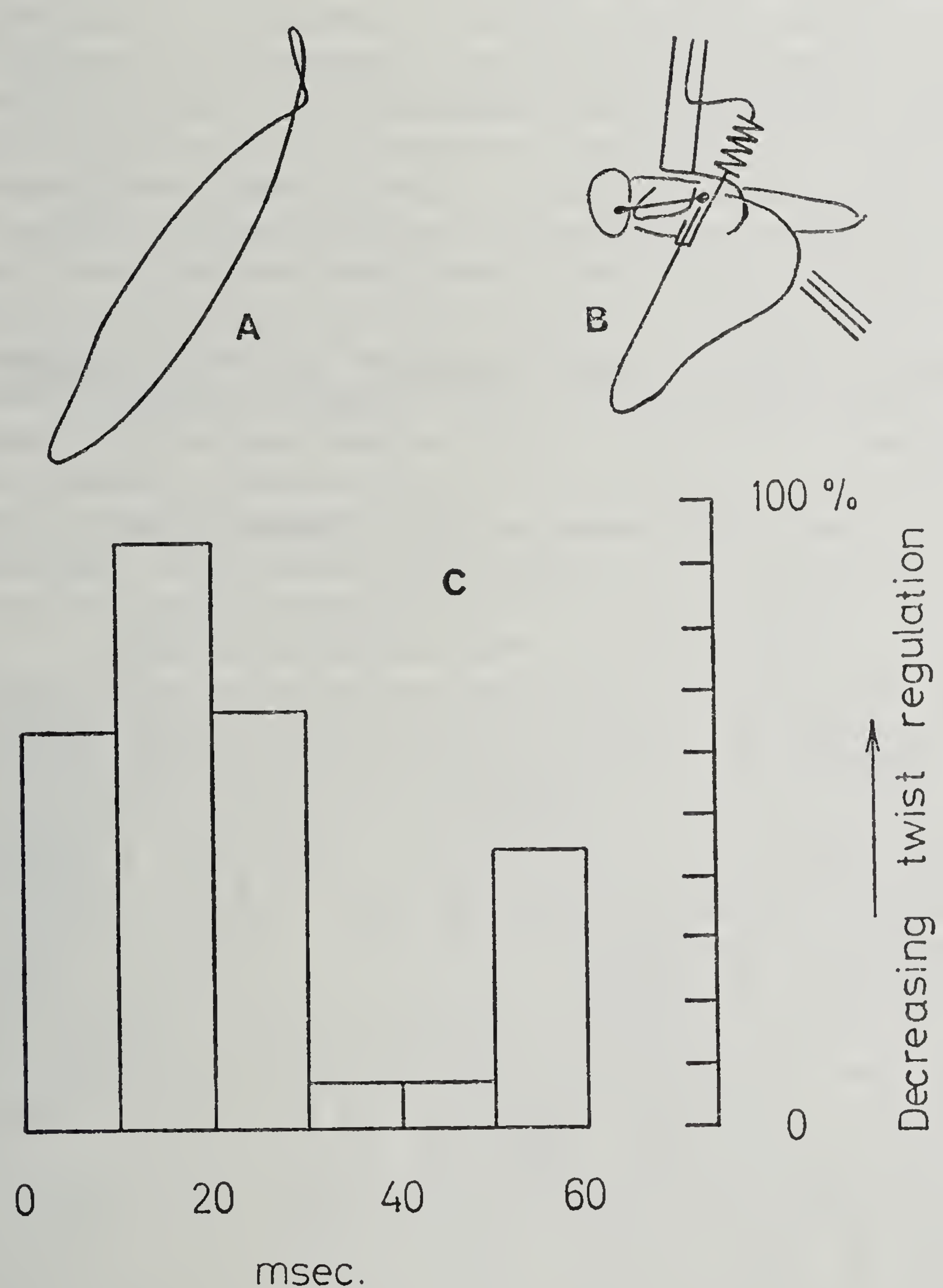

Fig. 2. The diagram illustrates the effect on forewing twisting of an anodic block applied to the hindwing sensilla. One wingstroke cycle is displayed, top position of the wing is at the left (c). (a) illustrates wingtip curve relative to body and (b) the electrode arrangement.

flight whereas the forewing groups, especially the proximal ones, are essential to control of angular movements around the three body axes, disclosing an organisation distinct from that found in higher Diptera (2).

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NERVOUS CONTROL OF INSECT FLIGHT

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In locusts the main flight muscles are of the fast twitch type and require nervous excitation to initiate each contraction during flight. It is thus necessary that the efferent command to these muscles be precisely structured in time in order to achieve the delicate co-ordination which characterises the wing movements. The muscles and skeleton, including the wings, constitute a resonant system whose oscillations are maintained by input energy from the muscles. Antagonistic sets of muscles contract in anti-phase. At low frequencies the two sets of muscles are activated either at the top or bottom of the wingstroke. Most units are activated by a single motor impulse, some units are silent. In order to increase frequency the muscles are excited earlier, i.e. the phase is advanced, so that the amplitude of the wingbeat is damped by the braking action of the muscles. Power per wingstroke is increased by recruiting silent units and by exciting some units two or three times in a single wingbeat.

The thoracic ganglia receive sensory input from moving thoracic parts during each wingbeat. Especially well known is the input from stretch receptors at the base of each wing. These fire one to several times during the late upstroke. At low frequency and large amplitude of wingbeat the stretch receptors produce several impulses beginning relatively early in upstroke, and as frequency increases the number decreases and the phase retreats. The stretch receptor input influences the wingbeat frequency in a negative feedback relationship. The input increases the wingbeat frequency, but high wingbeat frequency decreases the input. The effect of the input appears to be integrated over many cycles. The output is not noticeably sensitive to the phase of the input. With electronically controlled input *via* the stretch receptor nerves we have not been able to entrain the output rhythm.

Electrical stimulation of various parts of the nervous system reveals that without patterned input the thoracic ganglia can produce a co-ordinated output closely resembling the flight control pattern. However, it is also possible to elicit unco-ordinated activity, sometimes involving only a single motor unit. Under these circumstances the input-output relationships demonstrate such synaptic properties as temporal and spatial summation, accumulative refractoriness, frequency division, and after-discharge. Both the interval histogram characteristics for output due to random input, and the continuously variable intervals during after-discharge, suggest that the individual units have no oscillatory properties *other* than that due to the interplay of state of excitation and threshold recovery after discharge. Only when more output units than one are active do oscillations with characteristic frequencies appear. These appear to be due to neuronal interactions, but the type of interaction cannot yet be specified. Electronic analog models with either crossed excitation or inhibition between antagonistic neural elements, or combinations of excitation and inhibition, can all mimic the observed patterns. The most significant question for the immediate future study of the flight control system is, "how do the several tens of potentially independent motor neurons become locked into a rigid phase setting in the fundamental wingbeat oscillation?"

Some hint as to the answer to this question may come from study of the control of the myogenic insects. In flies the main wing muscles and skeleton also form a resonant system. Due to a specialisation of the muscle this system can oscillate at a frequency different from

the nervous excitation frequency. Characteristically a nervous frequency of several to 20 impulses per second produces a wingbeat frequency of more than a hundred per second. Since the timing of the contraction is not set by the nerve impulse the mechanical system in this case is input phase-independent. Furthermore, it is not necessary for the various muscles to receive their input according to any special sequence, and it is found that the phase and latency relationships between the motor impulses to different muscles are random. The only significant control parameter in the nervous pattern that remains is the frequency. In comparisons of the innervation of different muscles the system approaches the ideal pulse frequency modulation code. Within multiunit muscles, however, a phasic pattern is found. The several active units tend to fire at the same frequency but in different phases, even anti-phase, even though they must have synergic action. Until careful measurements of the duration of the "active state" are made for these muscles we can only speculate that the utility of this phasic distribution of the several units of one muscle is to smooth the power delivered at low innervation frequencies.

In some respects the fly resembles the locust whose flight motor neurons are uncoupled. In both, the individual units may run on their own schedule but they show positive frequency correlations with each other and with any known inputs. Even for the normal locust, in which the muscle pattern is highly phase dependent upon its innervation, it may be that these frequency correlations are the significant aspects of the nervous pattern as far as *variations* in flight activity are concerned. If all of the reflexes are like the stretch reflex, that is, phase insensitive, then only the frequency parameter is available for information transfer across the ganglion.

THE PHYSIOLOGY OF THE CENTRAL NERVOUS SYSTEM

THE PHYSIOLOGY OF INSECT AXONS

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Neurophysiology of insects is of special importance for at least two reasons: (1) Insects provide us with excellent opportunity to learn comparative neurophysiology because of their enormous variety in terms of morphology, physiology or behaviour; (2) To elucidate the mode of action of insecticides which are mostly neurotoxins, the basic aspects of insect nervous functions must be known. The electrophysiological technique would be useful to study at the cellular or even molecular level how nerve and muscle work, and to study how organ and animal are organised and work. For the former purpose the intracellular recording of membrane potential is of especial use, because it permits us to analyse the excitation phenomenon in terms of physico-chemical words such as membrane conductances, membrane ionic currents or the equilibrium potentials for sodium and potassium. In the present paper, the most basic aspects of insect cellular neurophysiology are described, and attempts are made to apply this knowledge to elucidating the mechanism of drug action on insect nerve on the one hand, and to extend it to the molecular level of excitation mechanisms on the other. The electrical properties of the cockroach giant axons have been analysed by means of intracellular microelectrode technique under a variety of experimental conditions.

It has well been established that the membrane resting and action potentials are described by the ionic theory advanced by Hodgkin and Huxley using mainly squid giant axons. This theory explains the action potential production by the transient increase in membrane conductances to sodium and potassium. The spike potential is followed by an undershoot or

positive phase which is terminated in a negative after-potential. Analyses have revealed that the negative after-potential is explicable by the accumulation of potassium released during activity in the immediate vicinity of the nerve membrane. The negative after-potential is liable to be affected by various experimental conditions. Its increase under certain conditions calls for mechanisms other than the potassium accumulation, such as the suppression of the potassium-activation by DDT, and the accumulation of an unknown substance near the membrane by allethrin.

The conditions that affect excitability may be classed into three groups depending on the mode of action: (1) Those which change the resting and/or action potential by simply altering the e.m.f. of the membrane. High-K and low-Na are typical examples; (2) those which are combined with or absorbed in the membrane; this is further divided into stabilisers and labilisers; (3) those which block excitability through the inhibition of energy metabolism, e.g. rotenone. We are here concerned with the group (2) above, i.e. the agents that attack the membrane. To elucidate their mechanisms of action, it is necessary to examine their effects on three parameters: the sodium-activation mechanism, the sodium-inactivation mechanism, and the potassium-activation mechanism. The fourth factor, the potassium-inactivation mechanism may be involved in certain cases. The ideal way of doing this would be no doubt to use the voltage-clamp technique which permits us to look at the sequence of events at the nerve membrane in terms of membrane ionic currents and membrane conductances. Although small diameters of axons have prevented us from applying this technique to insects, recent successful applications to the lobster giant axons which are only twice as large in diameter as the cockroach giant axons make us hope for its feasibility. However, it is also possible to analyse the mechanisms by means of the conventional intracellular microelectrodes. This is based on the observations (1) of the action potentials in terms of the height and the maximum rate of rise, the latter being indicative of the inward ionic current or the sodium-activation, (2) of delayed rectification by cathodal polarisation which is a measure of the potassium-activation, (3) of prolonged depolarising responses in Na-free K-rich media which is also a measure of the potassium-activation, (4) and of other properties and responses. Analyses along this line of approach with allethrin and tetrodotoxin (puffer poison) have shown that allethrin inhibits both the sodium-activation and the potassium-activation mechanisms at its blocking concentrations while tetrodotoxin inhibits the sodium-activation mechanism selectively without producing any effect on the potassium-activation mechanism.

There is no doubt about the view that the nerve membrane, about 100 Å thick, is the major site where various excitation phenomena take place. Calcium is known to bind with membrane molecules such as phospholipid, cholesterol and protein. An attempt was also made to gain insight into the molecular aspects of excitation with special reference to the role of calcium. Increasing the external calcium concentration made the applied cathodal depolarisation less effective in blocking action potentials. In other words, the curve relating the maximum rate of rise of the action potential to the membrane potential or the sodium-inactivation curve was shifted along the potential axis to lower membrane potential. The depolarisation by high-K also became less effective in blocking action potentials in the presence of high-Ca. This well accounts for the so-called K-Ca antagonism. Lowering the external calcium caused progressive depolarisation and block. It was, however, possible to restore excitability by anodal hyperpolarisation. These and other available evidences lead us to conclude that the integrity of the membrane molecular structure in which calcium works as a bridge between molceules must be maintained for excitability to persist.

THE EXCHANGES AND DISTRIBUTION OF IONS AND MOLECULES IN THE INSECT CENTRAL NERVOUS SYSTEM

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This communication is an attempt to define the chemical environment of the cells of the insect central nervous system. The nature of this environment is of particular physiological interest, for the exceedingly low sodium level and the relatively high concentrations of potassium and magnesium ions in the haemolymph of species from some largely phytophagous groups present certain difficulties in the interpretation of nerve function according to the classical membrane theory for the propagation of the action potential.

Despite great differences in the composition of the haemolymph the gross concentrations of the major inorganic ions in the central nervous tissues are essentially similar in *Periplaneta americana* and *Carausius morosus*. Similarly although the sodium level in the haemolymph of *Periplaneta* is an order greater than in that of *Carausius* the uptake of this ion into the nerve cord occurred at similar rates in the two species.

In both species the efflux of inorganic ions occurred as a two-stage process: an initial rapid phase eventually giving way to a slow exponential escape. The rapidly exchanging ions are identified as the extracellular fraction, the slowly exchanging ones as the intracellular fraction.

In *Periplaneta* the high concentration of cations, relative to chloride, in the extracellular fluid was found to be due to a Donnan equilibrium with the haemolymph. In *Carausius*, however, the distribution of the major cations, which included a very high concentration of sodium relative to that in the haemolymph, did not conform to a simple Donnan equilibrium. This departure resulted, in part, from a secretion of sodium ions into the extracellular system from the haemolymph. In the presence of dilute cyanide dinitrophenol the 10·6 concentration ratio with the haemolymph was abolished and the initial rapid uptake of ^{24}Na drastically reduced. The high extracellular concentration of potassium did not appear to result from any active processes and it is suggested that the activity of this ion may be lower than that in free solution.

Despite the high extracellular potassium concentration of 124·5 mM/l the equilibrium potential due to this ion was calculated to be approximately 37·1 mV due to the very high intracellular concentration of 555·8 mM/l potassium. The high extracellular sodium concentration of 212·4 mM/l maintained by the secretory processes produces an estimated equilibrium potential of 22·3 mV, which is roughly equivalent to the reversed phase of the action potential in cockroach giant axons.

It is thus apparent that despite the specialised ionic composition of the haemolymph in *Carausius* the extracellular environment of the central nervous system approximates to that of the body fluids found in other animal groups and is sufficient to maintain excitability according to the classical membrane theory.

THE FREE AMINO ACID POOL OF COCKROACH (*PERIPLANETA AMERICANA*) CENTRAL NERVOUS SYSTEM

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The free amino acids of cockroach thoracic and abdominal nerve cord have been extracted and estimated as described by Ray, 1964, in untreated cockroaches, in cockroaches prostrated by topical application of insecticides and in cockroaches paralysed by the injection of certain inhibitory substances. Table 1 shows the effect of insecticides on the composition of the free amino acid pool of nerve in the prostrate cockroach.

Table 1.

	Aspartate	*Glutamate*	*Glutamine*	*Alanine*	*Proline*	*γ-amino* n *butyrate*
Control	3·5	4·5	2·9	2·3	8·9	2·5
DDT	2·7	1·8	5·3	1·9	trace	1·8
DFP	4·2	3·3	5·8	8·0	1·7	3·2
o-IMPC	2·8	2·2	4·1	7·4	1·7	3·5
Dieldrin	5·1	3·9	8·7	4·2	1·6	3·0
n-Valone	7·7	1·2	trace	27·6	trace	2·1

DFP, di-isopropyl phosphorofluoridate; o-IMPC, o-isopropoxyphenyl-N-methyl carbamate; n-valone, 2-n-valeryl indandione.

The concentration of proline in the nerve of insecticidally treated cockroaches had fallen to a low level by the time they became prostrate. With the exception of valone the above insecticides cause hyperactivity and a stimulated oxygen consumption. It is likely that proline is oxidised as a result of this increased energy demand, some of the amino nitrogen appearing as glutamine as originally suggested by Winteringham (4). Valone lowers the rate of respiration and suppresses nervous and muscular activity. Valone is believed to inhibit pyruvate metabolism and it is possible that proline is oxidised to provide energy normally provided by pyruvate oxidation. Bursell (2) found that *Glossina* oxidised proline to give a quantitative yield of alanine during flight and it is possible that a similar pathway of oxidation is responsible for the increased alanine concentration in the nerve of insects poisoned with DFP, o-IMPC and dieldrin. With valone the alanine probably arises from pyruvate of glycolytic origin by transamination, some of the nitrogen coming from other substances than those considered here. The data for DDT are consistent with the idea that glycolysis fails during the later stages of DDT poisoning due to some non-specific effect, e.g., desiccation of the tissue, some of the alanine which had accumulated during the hyperactive stage now being oxidised instead of pyruvate from glycolytic sources. This idea is supported by the almost identical results in Table 2 for the amino acid concentrations of nerve from cockroach prostrated with iodoacetate which has been shown to inhibit triose phosphate dehydrogenase in nerve (1).

Table 2.

	Aspartate	*Glutamate*	*Glutamine*	*Alanine*	*Proline*	*γ-amino* n *butyrate*
Control	3·5	4·5	2·9	2·3	8·9	2·5
Iodoacetate	2·5	2·0	5·0	2·2	0·9	4·0
Arsenite	2·1	4·3	4·5	12·9	3·9	5·0
Fluoroacetate	3·5	3·0	4·0	8·0	3·3	4·2
Rotenone	2·8	6·4	2·6	14·1	8·1	4·4

Proline depletion has occurred when the normal pathways of glycolysis and Krebs cycle have been blocked by iodoacetate, arsenite or fluoroacetate. These examples add support to the idea that proline can act as a temporary metabolic reserve. Rotenone inhibits proline oxidation and so the concentration remains unchanged. The accumulation of alanine in the presence of arsenite and rotenone agree with the suggestion made in connection with valone poisoning that alanine represents the end product of glycolysis when pyruvate metabolism is blocked.

In the presence of fluoroacetate there is a ten fold increase in the citrate concentration in the nerve both in the intact insect and in the isolated nerve. This demonstrates the presence of the acetate activating enzymes, and the condensing enzyme and argues strongly for the presence of an active Krebs cycle in insect nerve.

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CONTRIBUTION TO THE ELECTROPHYSIOLOGICAL STUDY OF THE SIXTH ABDOMINAL GANGLION OF THE COCKROACH

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The often contradictory results obtained in effects of temperature changes on the synaptic transmission have caused us to study again the variations of the excitability threshold produced by temperature changes.

In the case of very slow temperature variations, a temperature increase applied to the cercal nerve induces an increased excitability and conversely. If this action is limited to the ganglion, the cercal action potential necessary to bring about the synaptic transmission is markedly smaller at a high temperature than at a low one. Moreover, the synaptic delay is shorter at a high temperature than at a low one.

If rapid temperature variations are used the cercal nerve excitability decreases for a temperature increase and vice versa. At the ganglionary level, a rhythmical activity sets in, rendering a more accurate study of the corresponding variations of excitability impossible. These results set several problems: first of all the question is to know which changes occur at the synaptic level when temperature variations are carried out at different speeds.

A concentration of 10^{-2} of -γ-amino-butyric acid (G.A.B.A.) provokes a complete inhibition of the response of the ascending giant fibres, though, at this concentration, the conduction of the action potentials along these fibres is not influenced by G.A.B.A. These results confirm those obtained for other nerve preparations of Insecta and Crustacea. β alanin has a similar action. At the same concentration, α-aminoβ-oxybutyric acid has no effect on the synaptic transmission.

-3-hydroxytyramine applied to the ganglion at a concentration of $5 \cdot 10^{-5}$ brings on bursts of action potentials propagated along the cord. Measurements of the amplitude and of the conduction speed of these action potentials show that the giant fibres do not seem to be involved. The involved fibres are long ones, some of which at least reach the mesothoracic ganglion. These results confirm Hess's (1) work founded on degeneration experiments.

A study was carried out in order to localise and dissociate different electrical phenomena observed by Yamasaki and Narahashi (2) with external electrodes set under the sixth abdominal ganglion of *Periplaneta americana*. The preparation was stimulated by the cercal nerve. The electrical activity was recorded with one microelectrode introduced into the ganglion, its ventral face desheathed. The positions of the microelectrode in the horizontal as well as in the vertical plane were located after each penetration.

Three different regions of the ganglion have been delimited:

A posterior one where a potential of cercal origin can be recorded. In the anterior part of this area presynaptic potentials, of a cercal origin, could also be observed.

A central zone, approximately corresponding to the neuropile is characterised by the appearance of post-synaptic potentials topped or not by a spike; the amplitude and the direction of these potentials change with the depth. Frequently the microelectrode tip induces a rhythmical activity followed in some cases by action-potentials propagated along the connectives. These potentials could originate at a certain distance from the cell-bodies.

In a larger and more anterior region, action potentials are recorded which, in view of their amplitude and their delay of appearance, could be electrotonically transmitted from the nerve fibres origin.

These results are difficult to interpret but we believe that histological studies involving a marking technique will bring about a better understanding in this field.

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THE CENTRAL NERVOUS CONTROL OF RESPIRATORY MOVEMENTS

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The control of the movements of spiracle valves has been studied in an attempt to understand the underlying central nervous mechanisms. In both the first spiracle (prothoracic) of the locust and the second (mesothoracic) of the adult dragonfly, power is supplied to the valve by a closer muscle which works against a cuticular spring. Relaxation of the closer allows the valve to open, and in the locust its gape is determined by the activity of a second muscle, the opener.

An endogenous pattern of activity, called "free running", occurs in the absence of ventilation in the two motor axons to the closer muscles of both the spiracles considered. It is characterised by a constancy of frequency and impulse interval, and by the lack of coupling between the units in one or in adjacent ganglia. Valve movements, synchronised with abdominal pumping strokes, are brought about by interneurones which run from ventilation "centres" to the motor neurones of the closer. In different species of dragonfly there may be one excitatory interneurone, or one inhibitory one, or both; when active they suppress free running usually for less than 25% of each ventilatory cycle. In the locust, three interneurones are probably involved and free running may play little or no part in the cycle. Of these, one is active during ventilatory pauses while the others fire during expiration and inspiration. This driven pattern of activity is characterised by approximately synchronous firing of the two units in one ganglion and sometimes in adjacent ganglia as well. Thus while the pattern in the motor nerves to the dragonfly spiracle is built up from free running and interneuronal activity, the latter alone is responsible for nearly all the activity in the locust, and free running may be observable only after section of the interneurones. Head and prothoracic CO_2-receptors, which are found in both species and affect free running more than the driven activity, play in consequence a greater part in the dragonfly than in the locust.

Carbon dioxide causes the valve to open in the dragonfly by a direct action on the muscle. Hypoxia, cooling and dilution of the haemolymph decrease the frequency of motor impulses to the closer and make it more responsive to CO_2. Conversely desiccation and heating increase the frequency and so reduce the muscular sensitivity.

In the locust the opener muscle receives two motor axons from the prothoracic ganglion and one from the mesothoracic. The prothoracic nerves fire during expiration whereas the mesothoracic nerve is active during inspiration: the activity of both may therefore produce a maintained contraction of the opener. In flight much of the opener activity is derived from the mesothoracic ganglion. This may have important consequences in allowing limited perfusion of the central nervous system with gases from the pterothorax resulting in appropriate ventilatory responses.

At rest, when only the prothoracic nerves are active, there may be a simultaneous cessation of impulses in the nerves to opener and closer muscles; however peripheral delays ensure that the opener contraction phase outlasts that of the closer so that the valve is wide open at the beginning of inspiration.

INSECT CENTRAL NERVOUS PATHWAYS

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Present day studies tend to concentrate on analysis at the single unit level and employ a number of techniques which are summarised below:

1. *Histological*
   (*a*) Staining of individual neurones—Methylene blue, Golgi.
   (*b*) Impregnation of all neurones—Other silver techniques, osmium—ethyl gallate, electronmicroscopy.
2. *Lesion or Ablation*
   (*a*) Whole nerve trunks.
   (*b*) Localised regions of ganglia or nerves.
3. *Degeneration*
   (*a*) Following microcautery of single cell bodies.
   (*b*) After section of nerve trunks.
4. *Electrophysiological* (Natural stimulation preferred to electrical)
   (*a*) Recording impulses of characteristic size and shape best using split nerve trunks.
   (*b*) Microelectrode recording and stimulation-mapping.
   (*c*) Intracellular electrodes best, because only single units:

$$\left.\begin{array}{l}\text{Axons}\\ \text{Somata}\end{array}\right\}\left\{\begin{array}{l}\text{direct stimulation}\\ \text{recording antidromic potentials}\end{array}\right.$$

DIFFERENT TYPES OF FUNCTIONAL PATHWAYS

Pathways in the central nervous system may be considered either (i) *direct* or through pathways when the axon passes through a given ganglion or (ii) *synaptic* where it is interrupted in the ganglion. Direct pathways demonstrated using electrical stimulation and recording may not necessarily be of functional significance and for this and other reasons it is important to employ natural stimulation wherever possible. Synaptic connections may be integrative, relaying (1:1), or multiplying. However, in no case has the type of connection been demonstrated in an insect using only single units. This does not matter in the case of integrative synapses for evidence that stimulation of many units gives rise to activity in a single post-synaptic neurone, is fairly easily obtained.

1. *Sensory-Motorneurone.*

Within a single ganglion these form segmental connections which can be regarded as the basic unit of the central nervous system. In insects the afferent fibres are separated into ventral and dorsal regions of the mixed nerve as was suggested by Hilton (3), Zawarzin (9) and others and has recently been demonstrated electrophysiologically by Fielden (1). She split the paraproct nerve of the last abdominal ganglion of the dragonfly larva and showed the presence of many small sensory units in the ventral region and large motor units in the dorsal region. After entering a ganglion, sensory fibres may ascend or descend a connective and this can lead to the spread of the input into intersegmental reflexes. Complex pathways can result because of descending motor axons in the connective.

2. *Sensory-Interneurone.*

The technique of splitting and recording from single units has been used in the abdominal nerve cord (2). This makes it possible to study the part of a neurone between regions where integration takes place. This type of work emphasizes the specificity of the connections between the sensory input and a given interneurone. Some interneurones only respond to a particular modality and to relatively small areas on single segments. Other multisegmental fibres respond to homologous areas on several segments. These results contrast with those obtained from histological studies which give a very diffuse picture in which it is difficult to conceive how such specific connections take place.

3. *Interneurone—Interneurone and Interneurone—Motorneurone.*

The giant fibre system of the cockroach (6) and dragonfly nymph (4) were used to illustrate these two types of connection. Although the cockroach preparation has been used a great deal there still remain aspects of its function which need further elucidation. The evasion response of the cockroach to a puff of air is reduced when it is repeated. This decline is partly due to the ability of the synapses in the metathoracic ganglion (7) but there is also an indication that there are adaptive changes in transmission through the last abdominal ganglion. This was shown by repeated applications of a constant puff of air and counting the number of spikes in the ascending giant fibres. When the puffs were repeated at intervals of half a minute there was a distinct decline in the response which recovered after a rest period. The presentation of puffs at five minute intervals showed no appreciable decline. This property is comparable to the so-called "adaptation" described by Pumphrey and Rawdon-Smith (6). It can be taken therefore that the simple learning process of habituation may occur in a single isolated cockroach ganglion.

INTEGRATIVE PROPERTIES OF SOME INTERNEURONES

The type of interneurone which responds multisegmentally has synaptic areas spatially separated in the ganglia of the abdominal cord. This means that impulses can pass up and down the interneurone following stimulation of different segments (5). In some cases it is possible, and this may be the primitive arrangement, that an interneurone has connections with both sensory and motor fibres in each ganglion. It is known from nerve cells of the mollusc *Aplysia* that impulses may pass in one direction and not another at the branches of single neurones (8). The hypothesis was suggested that a single arthropod neurone of this type might have integrative functions independently in each ganglion and only under certain conditions need invasion of the main axon of the neurone take place. In this way the integrative properties of an insect neurone might enable them to perform functions normally associated with several neurones. This is one way in which insects may have overcome the limitations imposed by the small number of central neurones.

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PROPRIOCEPTIVE REFLEXES AND THE CO-ORDINATION OF LOCOMOTION IN THE CATERPILLAR OF *ANTHERAEA PERNYI*

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This study was undertaken in order to discover the functional sphere of the dorsal muscle receptors of Lepidoptera, and if possible to show what special properties are conferred by the presence of an independent efferent innervation to these sense organs. As a preliminary to the investigation proper, the haemolymph inorganic cation composition was analysed in the relevant developmental stages. This information was used as a basis for formulating an experimental medium yielding electrophysiological responses similar to those seen in the animal's own haemolymph. The sensory responses of the muscle receptors (MRO) to constant velocity stretch were then examined in this saline. All stimulus waveforms yielded complex responses with tonic and phasic components; parameters signalled included "position", "movement" and "acceleration". Recording with an intracellular electrode in the receptor muscle (RM) gave, as with all other muscles tested, action potentials of the "fast" type only. The sensory discharge frequency from the MRO underwent a transient increase after each RM impulse. When successive stimuli were closely spaced, their effects summed, but no temporal facilitation was observed, either in the RM action potential or in the sensory discharge.

When the central connections of the RM were left intact, a tonic discharge was always observed. This could be inhibited by increased discharge frequencies in the MRO sensory axon but recovery from inhibition was rapid, and on release a post inhibitory "rebound" excitation was commonly seen. These reflex changes would tend to protect the sense organ from damage during intense stimuli, and to "take up the slack" in the released strand. Stretch of a single receptor yielded a strong excitatory intrasegmental stretch reflex, particularly in the dorsal longitudinal muscles. Intersegmental and crossed reflexes were also present, though weaker. Loads applied to the posterior end of the intact caterpillar were resisted in a manner strongly suggestive of a proprioceptive "resistance reflex". This was probably mediated by the MRO stretch reflex above, reinforced by additive and other interactions between reflexes mediated by adjacent excited MRO's. No conclusive evidence has yet been obtained for any role of these sense organs during larval locomotion other than such continuous modulation of effort in relation to load. The segmental MRO stretch reflexes are probably not essential to "propagation" of the wave of locomotor activity along the body in a "chain reflex" manner, though such effects may reinforce the contraction in successive segments.

THE CONTROL OF REFLEX RESPONSIVENESS AND THE INTEGRATION OF BEHAVIOUR

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Many of the actions and behaviour patterns of insects involve directly only relatively small parts of the central nervous system, such as one or a few segmental ganglia. Typically such "reflexes" can be elicited in full detail from an isolated part of the insect body. The integration of such reflexes as these into a coherent pattern of behaviour for the animal as a whole presents many problems. The end point of the integrative process is the fact that the responsiveness of a given reflex varies with respect to a constant stimulus. This control of reflex responsiveness is discussed here.

A concept of cerebral integration, while supported by some of the known facts, is inadequate as a complete explanation. Firstly, it merely shifts the site of the mechanism, rather than explaining it, and secondly, decapitation does not result in the disorganisation of the reflex structure of the rest of the nervous system. This shows that the control of responsiveness is diffuse in the CNS.

A convenient preparation is found in the prothoracic grooming reflex of grasshoppers (2 and 3). Receptors, integrative mechanisms and effectors are all confined to one segment; any extra-ganglionic influence must be transmitted through the readily accessible connectives. Under standard experimental conditions, the response cannot be elicited, i.e. it is completely inhibited, if the CNS is intact. When the connectives joining the prothoracic ganglion to the rest of the nervous system are cut, responsiveness rises to almost 100%, i.e. it is completely disinhibited. The source of this inhibitory input from the CNS to the prothoracic ganglion has been examined by lesion experiments, and its nature by electrophysiological and anatomical means. The influence of the posterior chain (mesothoracic, metathoracic and abdominal ganglia) is discussed here.

Lesions which reduced progressively the amount and activity of the posterior CNS connected to the prothoracic ganglion resulted in a progressive disinhibition of the ganglion, seen in the rise in reflex responsiveness. Symmetric and asymmetric lesions gave divergent results, which lead to the postulate of negative feedback (mutual inhibition) between the two halves of the prothoracic ganglion. This agrees with the postulate of Weiant (4) to explain a different circumstance in the metathoracic ganglion of the cockroach, and suggests that the objections brought by Roeder *et al.* (1) are unfounded. Experiments on the head ganglia give broadly similar results as to their effect on the prothoracic reflex.

It is concluded that the inhibitory input to the prothoracic ganglion is derived from all parts of the CNS, rather than from any particular source, and that it varies according to the activity of any part: if activity in a particular area is increased, this part will exert a greater inhibitory influence on the prothoracic ganglion. This conclusion is supported by stimulation experiments. Two alternative hypotheses to explain this are examined. The first postulates specific inhibitory connections between the systems examined, possibly by a single interneurone. The second suggests a more generalised effect without specific connections, by which it is thought that the activity of any specific functional mechanism will to some degree inhibit all others, and especially those with which it shares functional parts. Such a state of affairs must obviously be modified in specific cases, but is suggested as a general rule. In this case the inhibition would be a function of the total signal input to the prothoracic ganglion.

The first hypothesis is difficult to test. The second, however, leads to postulates as to the nature of the inhibitory input which may be tested. If inhibition in the prothoracic ganglion is a function of all signal arriving at it, then reduction of the signal by the lesion technique described should lead to a reduction in the amount of signal, but not to differences of kind. Degeneration techniques and electron microscopy are being used to investigate the anatomical nature of the input to the ganglion, and electrophysiological techniques to investigate the signal flow. Data are as yet incomplete, but allow a tentative support for the latter hypothesis, that the inhibitory influence is a function of all arriving signal, not merely of a certain element of it.

In the course of this work it has been found that the activity of a ganglion is profoundly influenced by the input which it receives, to the extent that complete absence of input may result in abnormally high levels of "spontaneous" activity, often of a highly rhythmic and patterned nature. It is dubious whether such activity is ever seen in the normal nervous system, or whether it has any correlation with normal effector action. Because of the importance of leaving the preparation with its normal interconnections, it is not desirable to dispose of unwanted signal in a connective by cutting it prior to recording, as this may grossly alter the desired signal as well.

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BRAIN CONTROLLED BEHAVIOUR IN ORTHOPTERA

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The brain of orthopterans is known to be an important link in the control of uni- and plurisegmental behavioural activities organised within the ventral nerve cord. In crickets (*Gryllus campestris* L.) evasive behaviour consists of kicking movements carried out with the hindlegs and followed by forward locomotion. This activity can be elicited through mechanical stimulation of the anal cerci. The sequence of neural events underlying this response is summarised as follows: Sensory signals arriving from the cerci evoke giant fibre responses within the abdominal cord which are propagated to the metathoracic ganglion and transmitted to motor neurons supplying the leg muscles. During certain states of sexual activity, however, the cercal response disappears which indicates that kicking can be inhibited.

Inhibition of the kicking response has also been observed during focal electrical stimulation of fibres within the mushroom bodies of the protocerebral ganglia. Electrophysiological studies were carried out to find the area in which inhibitory commands from the brain affect the synaptic transmission in the ventral cord. The results show that descending inhibitory commands do not change the synaptic properties within the last abdominal ganglion although the male is unable to move the hindlegs. It seems therefore that inhibition takes place at the second junction, e.g. the synapse within the 3rd thoracic ganglion. Further analysis is in progress.

Male crickets are unable to stridulate in a normal way as soon as dorsal parts of the two mushroom bodies in the protocerebrum are removed or if the central body neuropile is destroyed with HF-coagulation. Electrical stimulation within these regions of the cricket brain extended the results obtained from ablation experiments. Loci have been found stimulation of which caused a suppression of singing, and other points which evoked stridulation similar to that male crickets usually produce. However, there exists a difference in the reaction whether electrical shocks are applied to the mushroom body interneurons and tracts entering there or to the central body fibre network. In the first case neural mechanisms are switched on or off related to the formation of normal calling and fighting songs, while stimuli applied to the central body lead to significant changes in the temporal patterning of sound pulses emitted through atypical elytral movements. The central body neuropile is believed to be closely related to neural systems responsible for pattern formation in acoustical behaviour of crickets.

These studies indicate two ways in which the brain can operate. In the evasive behaviour brain neurons control a segmentally organised pattern by inhibitory commands which seem to suppress the signal transmission within the 3rd thoracic ganglion. Sound production of male crickets depends on both inhibitory and excitatory brain systems determining duration and strength of chirping and the patterns of wing movements belonging to the different types of songs.

METABOLISM

BIOSYNTHESIS OF PHOSPHOLIPIDS IN INSECTS

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Previous investigations of insect phospholipids have shown that, with certain minor exceptions, these compounds do not differ qualitatively from those in other animals. The blowfly, *Phormia regina*, is unusual in that phosphatidylethanolamine constitutes at least 65 per cent of the phospholipids of the egg, larva or adult. In the larva of this organism the choline-containing phospholipids are replaced by lipids containing β-methyl choline when the dietary choline is replaced by carnitine or γ-butyrobetaine. The present communication reports on the origin of phospholipid ethanolamine, the biosynthesis of phosphatidylethanolamine, and the molecular relationships between dietary substitutes for choline in *P. regina*. Comparative studies on *Protoparce sexta*, *Trichoplusia ni* and *Prodenia eridania* are included.

The phospholipids of *P. regina* larvae reared on media containing carbon^{14}-labelled ethanolamine, serine, glycine, or formate were examined by silicic acid chromatography. The hydrolysis products of the phospholipids were identified by paper chromatography and the identity of ethanolamine confirmed by the preparation of the phenyl dithio*iso*cyanate derivative. The results indicate that ethanolamine can be synthesised by pathways known from other organisms: condensation of glycine and a C-1 unit to form serine; decarboxylation of serine to yield ethanolamine. Alternate pathways of ethanolamine metabolism involving deamination also occur.

C-^{14}-labelled ethanolamine injected into larvae or adults of *P. regina* is incorporated into phospholipids and into expired CO_2. Experiments using isolated fat body show these pathways to occur in this tissue. Comparative experiments with the larva of the Lepidoptera *Protoparce sexta*, *Trichoplusia ni*, and *Prodenia eridania* indicate that similar pathways occur. Ethanolamine is incorporated most rapidly into the lipids of the fat body although the gut contains more phospholipid than other tissues. Phospholipids synthesised in the fat body are apparently released into the hemolymph.

Choline analogs of the following types have been tested as dietary substitutes for choline and as growth antagonists: $(CH_3)_3\overset{+}{N}(CH_2)nCH_2OH$; $(R)(CH_3)_2\overset{+}{N}CH_2CH_2OH$; $(R)_2(CH_3)\overset{+}{N}CH_2CH_2OH$; $(R)_3NCH_2OH$ $(R = CH_3\text{-}C_4H_9)$. The results of this and previous studies indicate that the following characteristics must be present in order to substitute for choline in the larval diet of *P. regina*: two N-methyl groups must be present while the third alkyl group can vary from none to C_4H_9; if a terminal hydroxyl group is present the carbon chain must be two carbon atoms long. It is not known how many of the successful choline substitutes are incorporated without change into phospholipids although earlier work demonstrated that 2,2-dimethylaminoethanol, β-methyl choline and 2,2-dimethylamino*iso*propanol are.

The compound $(CH)_3\overset{+}{N}CH_2CH_2CH_2OH$ is a growth antagonist when *P. regina* larvae are reared on medium containing carnitine or γ-butyrobetaine in place of choline but not in the presence of choline. Apparently this compound is an inhibitor in the metabolic pathway which results in the formation of β-methyl choline.

Isolated fat body or fat body homogenates of *P. regina* larvae incorporate ethanolamine, choline and carnitine into phospholipids. Larvae raised on methyl-C^{14}-carnitine contain β-methyl choline, carnitine and two unidentified metabolites. Almost no incorporation from C^{14}-carnitine occurs when choline and carnitine are present in equal amounts in the medium.

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(The investigations on dietary substitution of choline by various analogs have been accepted for publication by the *Journal of Insect Physiology*.)

LIPID TRANSPORT, CONVERSION AND CATABOLISM IN *HYALOPHORA CECROPIA* (LEPIDOPTERA)[1]

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The 21-day period during which an *H. cecropia* pupa develops into an adult moth of completely different morphology, is one in which a great amount of energy is required for the synthesis of adult structures. Although lipid is the major substrate in these insects, it is metabolised only after the 17th day of development in the male and is the prime substrate for flight in the adult. The female on the other hand utilises lipid after the first week of adult development and contains only a small amount after eclosion. The lipid content of the male moth which may comprise more than 60% of the dry weight of the animal on the first day of adult life, drops precipitously between the second and fifth day of adult life. Our data indicate that lipid (the majority of which is triglyceride) is conserved during adult development for later use as an energy source for flight.

The following data corroborate the suggestion. Flight muscle homogenates display an RQ indicative of lipid catabolism; flight muscle homogenates and isolated sarcosomes actively oxidise exogenous C^{14} labelled fatty acids and Kreb's cycle intermediates, but not glucose or pyruvate; the oxidising capacity of flight muscle homogenates was reduced 90% by dialysis, but the addition of ATP, Mg and citrate restored activity to normal; these cofactors were also necessary for normal mitochondrial oxidation; fatty acid activating enzymes are highly active in flight muscle.

Although those long chain fatty acids so vital to flight muscle metabolism are stored as triglycerides in the fat body, they are released into the hemolymph as diglycerides. This phenomenon of diglyceride release was demonstrated by pre-labelling the neutral lipid of the fat body with C^{14} palmitate and following its release into the hemolymph both *in vivo* and *in vitro*.

The release of diglyceride from fat body appears to be an endergonic process since it is almost completely halted by the addition of metabolic inhibitors. When the process is inhibited, free fatty acids passively diffuse from the fat body into the hemolymph. The release of diglycerides *in vitro* is specific for insect hemolymph while free fatty acids and triglycerides will diffuse into artificial incubation media as well. Electrophoretic studies suggest that these diglycerides are conjugated to one specific hemolymph lipoprotein and carried to the flight muscle where the fatty acids are liberated. This may be a common mechanism for lipid transport in insects since we have shown it to be the case in *Melanoplus* and *Periplaneta* as well as *H. cecropia* pupae and adults.

The mechanism by which fatty acids are cleaved from the diglycerides in the blood is still unknown. Although various tissues of *H. cecropia* show potent esterase activity toward triacetin and tributyrin, no *true* lipase activity could be demonstrated against the insoluble glycerides of higher fatty acids by conventional techniques. By the use of a new lipase assay utilising Florisil column chromatography and liquid scintillation spectrometry, we have demonstrated low but definite lipase activity in both fat body and flight muscle. Diglycerides are hydrolysed by the enzyme in the presence of calcium ions, and this may be the means by which fatty acids are made available to the flight muscle sarcosomes.

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EFFECT OF PHOTOPERIOD AND TEMPERATURE ON FATTY ACID COMPOSITION OF THE MOSQUITO *CULEX TARSALIS*

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Prolonged exposure to extremes of temperature results in changes in the degree of saturation of lipids in insects. This has been well substantiated by a number of investigators, such as Munson's finding that between 27 and 31°C, a marked change occurs in the iodine number of lipids in the American cockroach. House *et al.* related fat saturation of dietary lipid to survival at high temperature in the parasitic fly, *Pseudosarcophaga affinis*. From these findings it is clear that exposure at low temperature, such as hibernation conditions, coincides with an increased proportion of unsaturated lipids. Since natural hibernation also includes exposure to short photoperiod, the interrelationship between photoperiod and temperature was studied in adults of the mosquito *Culex tarsalis* Coq.

The strain of *C. tarsalis* tested was derived from stock originating near Bakersfield, California (35°N latitude), and is much less cold resistant than a strain originating near Pullman, Washington (47°N, unpublished observations). It has been shown that adults of this strain increase fat body size at 8 hour photoperiods in comparison to 16 hour daily photoperiods (3). Accordingly these two extremes of photoperiod were used with the following combinations of temperature: (1) All stages at 22°C (considered as standard conditions); (2) all stages at 30°C; and (3) larvae and pupae at 22° with an inclusion of 5° for three days and 11° for 2 days starting with the second instar, adults at 14° for 3 days, 10° for 3 days, and 6° for 5 days. Larvae were reared on dog food or a diet based on herring meal, adults fed on 10% sucrose.

Fatty acids of a chloroform-methanol extract were prepared and identified by gas chromatography. On 16 hour photoperiod at 22°C fatty acid composition of larvae resembles that found in *Aedes aegypti* (1), and of adults that found by Van Handel and Lum (2) in *Aedes taeniorhynchus* (6). In adults the principal unsaturated fatty acids are palmitoleic and oleic. At standard conditions following 21 days of adult life the females contain 41% and 22%, males 38% and 17% respectively of these two fatty acids.

When high and low temperature is combined with long and short photoperiod it can be seen that temperature has a major effect on relative amounts of palmitoleic and oleic acids, but that the interrelationship of photoperiod is also evident. Differences between males and females become greater, which might be expected since only females hibernate successfully. For females the combination of low temperature and short photoperiod at 8 hour daily photoperiod yields 43% and 26% of palmitoleic and oleic acids respectively. Long photoperiod at low temperature yields 31% and 19% respectively. Combinations of long and short photoperiod at high temperature result in lower amounts of both these unsaturated fatty acids, and in increased amounts of palmitic acid. It is thus apparent that lipid reserve synthesis of *Culex tarsalis* in preparation for hibernation is affected by photoperiod as well as temperature.

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ACCUMULATION OF CITRIC ACID WITH AGE IN HOUSE FLIES

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High citric acid concentrations have been reported in insects (2, 4, 5 and 6). We found a substantial increase in citric acid content with age in house flies *Musca domestica*. Other diptera such as the Mediterranean fruit fly *Ceratitis capitata* and the yellow fever mosquito *Aedes aegypti* were also examined.

Flies were fed water and sugar. Mosquitoes were fed honey. All insects were kept at 26°C and 60 to 70% relative humidity. Whole female insects were homogenised in 5% trichloroacetic acid, and citric acid determined by a modification of the method of Natelson *et al* (3).

The yellow fever mosquito showed the highest citric acid concentration of the species examined. Citric acid increases with age in the house fly and in the fruit fly (fig. 1). There was a decline in the beginning, the lowest point being approximately at 1 day for the house fly, at 4 days for the fruit fly, and at 7 days for the yellow fever mosquito. The citric acid contents of pupae were only measured in one experiment. The relatively high concentration of 1·2 μM/g was found, declining to 0·73 μM/g for just emerging flies.

The present work confirms that high concentrations of citrate could be considered a biochemical characteristic of the class Insecta (1 and 2) as compared to other animals (7 and 8).

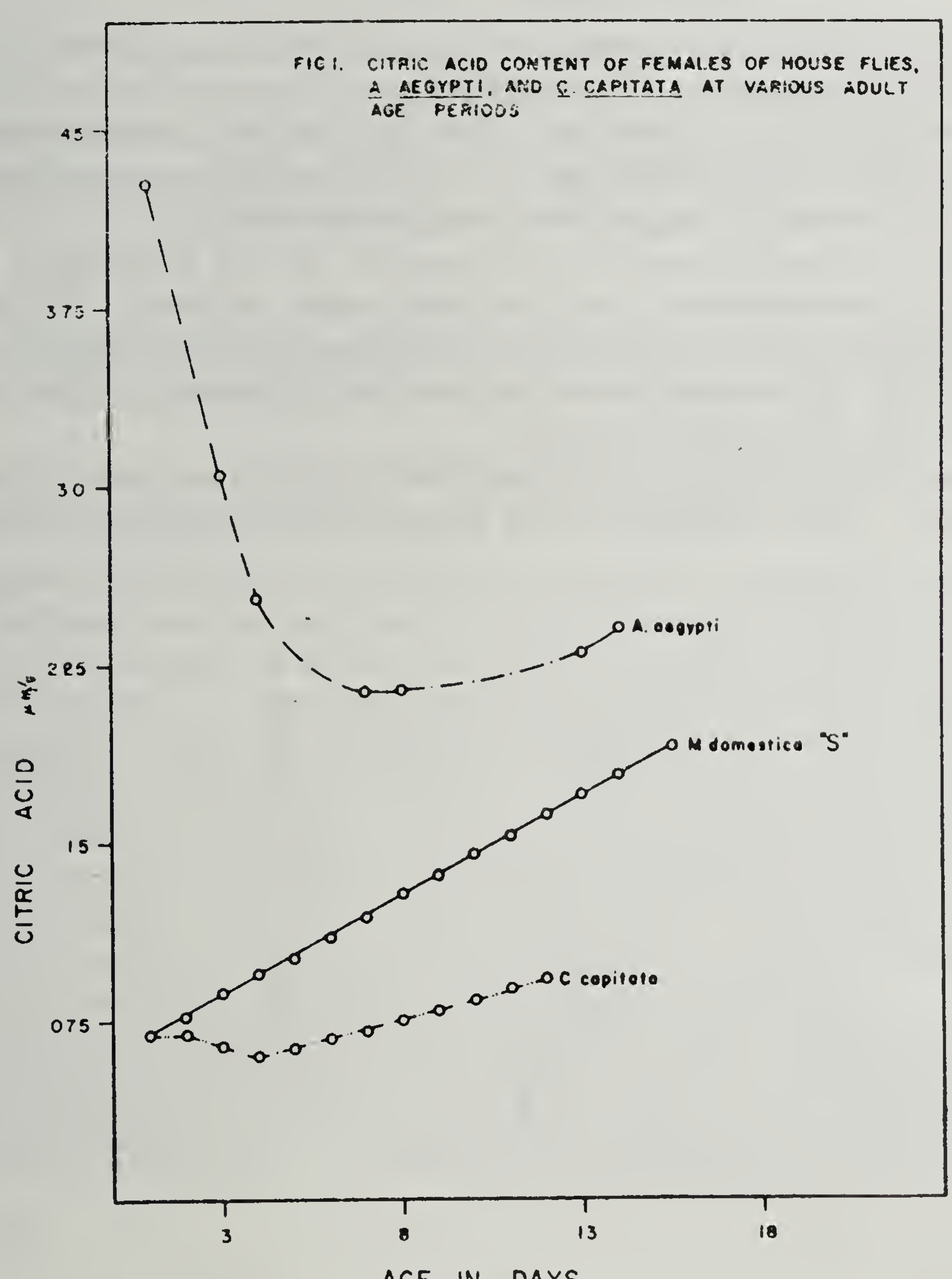

Fig. 1. Citric acid content of females of house flies, *A. aegypti*, and *C. capitata* at various adult age periods. Each point is based on 4 determinations and constitutes an average of 5 to 6 experiments for houseflies, 3 for *C. capitata*, and 2 for *A. aegypti*.

Approximately linear increases in citrate concentration with age were observed in the house fly and in the fruit fly. Flies showing signs of senescence possessed especially high citric acid concentrations. While no correlation could be proven between citrate concentration and age in the yellow fever mosquito, here too citrate increased shortly before death.

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BIOCHEMICAL INVESTIGATIONS OF THE MORPHOLOGICAL COLOUR CHANGES IN *MANTIS RELIGIOSA* (DICTYOPTERA)

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Morphological colour change in *Mantis religiosa* is well-known, but there is no satisfactory explanation of the phenomenon from the physiological and biochemical standpoint. Okay has tried to identify the pigments in the integument of green and of brown individuals and our results are in accordance with his findings. In the following report we should like to point out some of the observations that might be especially interesting.

Four groups of compounds seem to be responsible for the pigmentary colouring in this species: carotenoids, ommochromes, pteridines and a bile pigment. The separation of the substances was made by paper and column chromatography: for those that could not be adequately separated in this manner, special methods had to be used. The amount of pigment could be concluded from the extinction curves.

The blue-green bile pigment is to be found only in the green colour phase and is absent in brown individuals. This substance has a characteristic absorption spectrum, similar to

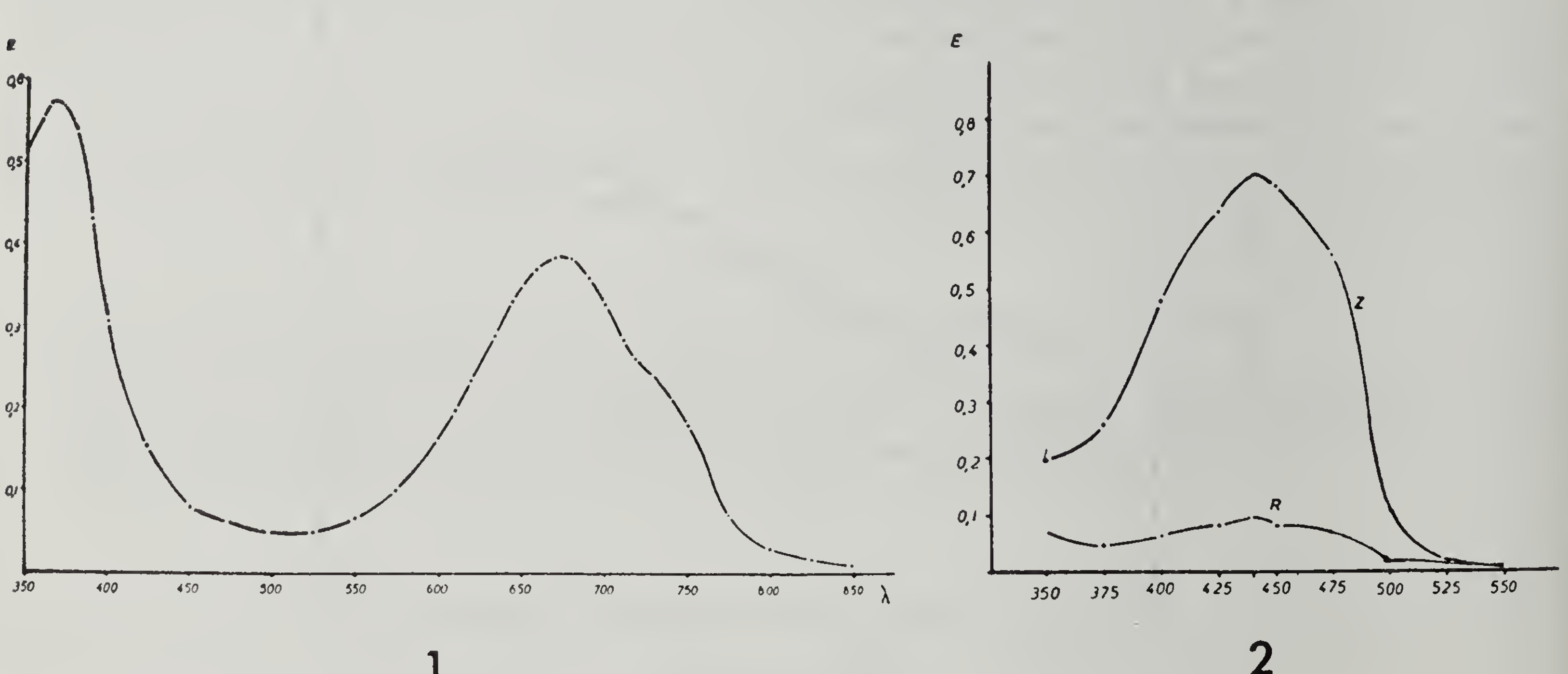

Fig. 1. Absorption spectrum of the blue-green bile pigment. Solvent $CHCl_2$.

Fig. 2. Absorption spectra of the carotenoids from green (Z) and brown (R) animals. Solvent light petroleum.

that of mesobiliverdin. (fig. 1). It seems to be very unstable when treated with oxidants and gives a positive Gmelin reaction. In the green animals, the amount of ommochromes is very small and an inverse correlation between the ommochromes and the bile pigment is possible.

A remarkable difference between the green and the brown colour phases was found in the quantity of carotenoids. The total amount of carotenoids in the integument of brown individuals is about 5 to 7 times smaller than the amount in green individuals (fig. 2). The chromatographical separation showed that there are three different compounds in green and only two in brown animals. Owing to the fact that there is no difference between the food of green and of brown individuals and that in animals the formation of carotenoids "de novo" cannot be accepted, it must be supposed that this is a result of differences in the metabolic rate in both colour phases. It may be, perhaps, a difference in decomposition and storage of carotenoid compounds. Carotenoids obviously play an important part in the colouring of *Mantis*, and this statement must be considered as different from the findings on the locust *Schistocerca gregaria*.

The last group of pigments involved in the colour change are ommochromes. We were not able to separate them from one another, but as a group they correspond to the "insect-orubin", described by Goodwin from *Schistocerca gregaria.* Besides the fact that the quantity of ommochromes in brown animals is much greater, yet another important consideration must be taken into account. It is known that ommatins can be reduced to red dihydro ommatins and that both states of oxidation can occur in the same species. There is reason to believe that the oxido-reduction of these compounds participates in the colour change: but this has yet to be proved. Pteridines, appearing on the paper chromatograms as fluorescent zones, have no significant part in the colour of these animals as a whole.

Thus, the combinations of pigments in *Mantis religiosa* are as follows: green individuals—carotenoids, bile pigment, ommochromes (few), pteridines; brown individuals—carotenoids (few), ommochromes (many, partially reduced), pteridines. It should be noted that three principal colour components (yellow, blue-green and reddish-brown) are present and accounts for the production of the large number of colour variants.

CHEMICAL CHARACTERISATION OF THE SCENT OF THE GREEN VEGETABLE BUG, *NEZARA VIRIDULA* (HETEROPTERA)

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With information derived from the use of gas, thin layer and paper chromatography and infrared, ultraviolet, mass and nuclear magnetic resonance spectrometry, structures have been assigned to 18 of the 20 constituents of the scent of *Nezara viridula.* These constituents comprise over 99·9 per cent of the scent. This defensive scent is thus revealed as by far the most complex mixture so far reported. The scent consists of two phases one yellow and one clear, and is stored in a single median, metathoracic reservoir. The following compounds were present: *trans*-2-unsaturated aldehydes (of chain length C_3, C_4, C_6, C_8 and C_{10}) and the corresponding *cis* C_{10} compound; saturated (C_4, C_6, C_9) and one unsaturated (C_6) ketone, dicarbonyl compounds (4 keto hex-2-enal), 4 keto oct-2-enal) acetate esters (corresponding with the C_6, C_8 and C_{10}-2-enals) and normal paraffins (C_{11}, C_{12}, C_{13}). Of these the dicarbonyl compounds do not appear to have been described before in the chemical literature.

The clear phase is largely non-polar, being composed of some 72 per cent of tridecane and dodecane. These paraffins have a limited miscibility with the more polar compounds which, being present in excess of this amount, form a separate, denser, yellow phase.

ADAPTATION OF INSECTS TO TOXIC PLANTS

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Insects can avoid the toxic effects of tobacco alkaloids by a number of different mechanisms. Previous investigations have established that the green peach aphid, *Myzus persicae*, avoids the alkaloid-containing xylem and feeds selectively in the phloem. This communication is concerned primarily with the excretory mechanism by which the tobacco hornworm, *Protoparce sexta*, and other lepidopterous larvae maintain a low concentration of nicotine in the hemolymph and with the metabolism of nicotine and nornicotine to other alkaloids shown by other insects which feed on tobacco. Comparative studies on insects which do not feed on tobacco are included.

Following transfer of fifth instar tobacco hornworms to tomato foliage to eliminate tobacco alkaloids from the body, nicotine can be administered orally, topically and by injection. In each case, nicotine appears rapidly in the feces and the rise in blood nicotine is transitory. The identity of the excreted nicotine was confirmed by paper and gas chromatographic comparisons and by ultra-violet and infra-red spectroscopy. When larvae are allowed to completely consume one of each of several carefully paired tobacco leaves, the alkaloid content of the feces is virtually identical with that of the uneaten leaf. This mechanism appears to operate in other lepidopterous larvae which feed on tobacco such as the tobacco budworm, *Heliothis virescens*, and the cabbage looper, *Trichoplusia ni*.

The ability of the tobacco wireworm, *Conoderus vespertinus*, the cigarette beetle, *Lasioderma serricorne*, and the differential grasshopper, *Melanoplus differentialis*, to metabolise nicotine has been investigated. These insects produce one, two, and four metabolites respectively. In each case the most important appears to be cotinine. The housefly, *Musca domestica*, an insect which does not normally feed on nicotine also produces cotinine as the principal metabolite of nicotine. The identity of cotinine has been confirmed by paper chromatographic comparisons and by ultra-violet and infra-red spectroscopy. The second most important metabolite of nicotine from *M. differentialis* may be cotinine methonium ion.

In vitro experiments using the housefly indicate that the oxidation of nicotine to cotinine occurs in the microsomes and requires a reduced pyridine nucleotide and oxygen. The ability of adult houseflies to metabolise nicotine decreases markedly with age.

In contrast to lepidopterous larvae which feed on tobacco, the southern army worm, *Prodenia eridania*, has been reported to produce a large number of alkaloid metabolites from nicotine. The development of two-dimensional, thin-layer chromatographic techniques for alkaloid separation and identification has made possible a re-examination of this problem. The two principal metabolites appear to be cotinine and nornicotine. While cotinine is not metabolised further, some of the other metabolites may arise from the further metabolism of nornicotine.

It seems clear that if the metabolism of nicotine to less toxic alkaloids enables some insects to feed on tobacco, it is the extent rather than the nature of the reactions which represents a specific adaptation to this particular host plant.

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(The studies of the tobacco hornworm have been accepted for publication by the Journal of Insect Physiology.)

HORMONAL ACTIVATION OF FAT BODY PHOSPHORYLASE IN DIFFERENT IONIC MEDIA

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Cahill *et al.* (1) have shown that glycogen synthesis and degradation in liver slices incubated *in vitro* is affected by the relative concentrations of Na^+ and K^+. In view of these findings we have investigated the effect of these ions on phosphorylase activity and the hormone mediated changes in activity of this enzyme in cockroach fat body (3).

In common with the findings of Cahill *et al.* (1) it has been shown that the fat body of the cockroach (*Periplaneta americana*) has a higher rate of glycogenolysis when incubated in a saline solution containing 0·15 M NaCl than in one in which the NaCl is replaced by KCl. This result may be explained by the known inhibitory effect of Na^+ on phosphorylase phosphatase (2). A reduction in tissue Na^+ would be expected to result in decreased inhibition of phosphorylase phosphatase and a concomitant decline in the amount of active phosphorylase. This assumption has been shown to be true. Fat body incubated in saline containing KCl but lacking NaCl has a lower phosphorylase activity than tissue incubated in a similar manner in a saline solution containing NaCl instead of KCl.

The preincubation of tissues in a K^+ rich medium is a useful device for lowering phosphorylase activity to its lowest possible level. This is particularly important when studying the effects of the hyperglycaemic hormone on the enzyme. If tissue is first preincubated in a high K^+ medium and then transferred to a high Na^+ medium in which is included hormone it is possible to demonstrate a pronounced activation of phosphorylase. This appears to be due to the initial low level of phosphorylase activity obtained by preincubation in the high K^+ medium. On transfer to the high Na^+ medium in the presence of hormone the active form of phosphorylase can accumulate as a result of increased inhibition of phosphorylase phosphatase due to the return of Na^+ to thè tissue. The increase in enzyme activity induced by the hormone in the high K^+ medium is only about 25% of that obtained in the high Na^+ medium. These results may also be explained by the inhibitory action of Na^+ on phosphorylase phosphatase.

The explanation of the effect of Na^+ and K^+ on phosphorylase activity presupposes that the ionic composition of the incubation media reflects the concentration of those ions in the tissues. Measurements of Na^+ and K in fat body have shown that preincubation in the high K^+ medium does result in a lowering of Na^+. Also, the return of the tissue to the high Na^+ medium does result in a tissue concentration of this ion much above normal levels.

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NEUROSECRETION

SOME ENDOCRINOLOGICAL ASPECTS OF THE LARVAL DIAPAUSE IN RICE STEM BORER, *CHILO SUPPRESSALIS*

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It has been concluded from the results of our experiments, that the larval diapause of the rice stem borer is controlled by the secretory activity of the corpora allata (1).

Recently it was shown that the brain taken from diapausing European corn borer larva is capable of terminating the larval diapause of this borer (2). In the case of the rice stem borer, however, somewhat different results were obtained in a similar experiment. The diapause was not terminated by the implantation of the brain from the diapausing larva, though some shortening of the time before pupation was observed, while the brain from diapausing larva caused the pupation of decapitated, diapausing larva in 21 days on an average. On the other hand, the implantation of the brain-corpora cardiaca-allata complex obtained from a diapausing larva into a decapitated one, did not induce pupation but resulted in the maintenance of the larval diapause. In this connection farnesol which is known to show juvenile hormone-like action in various insects, was topically applied to the rice stem borer in post-diapause. The mortality of the larvae treated with farnesol was considerably higher than that of the controls but it was clearly indicated that the period before pupation of the former was prolonged for twice as long a period as in the latter.

In another experiment the diapausing larva was ligated behind the head under a strong pressure to the head from both dorsal and ventral sides, and brain alone moved to the prothorax, leaving the corpora cardiaca and allata in the head. In this way the brain could be separated perfectly from the corpora cardiaca and allata. Such treatment induced the termination of diapause in some individuals.

These facts seem to suggest that corpus allatum or juvenile hormone plays some role in the maintenance of diapause and the inactive brain can be changed to an active one in the diapausing larva lacking corpora allata.

As a trial to approach the solution of this problem some model experiments were carried out using physiologically vital active substances such as cholesterol, diethylstilbestrol, noradrenaline, progesteron, and hexestrol, which were proved to act on the silk-worm *Bombyx mori* just like the brain hormone (3). When $0{\cdot}002$-$0{\cdot}2\gamma$ of these substances was injected into diapausing *Chilo* larvae, neither pupal nor larval moulting occurred, while, on the contrary, cholesterol, diethylstilbestrol and noradrenaline could induce the larval moulting to a certain extent in the headless larvae. Needless to say, they were unable to induce the pupation of the isolated abdomens.

From the results mentioned above, it may be assumed that these chemicals can stimulate the prothoracic gland to release the moulting hormone only in the decapitated larvae.

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NEUROSECRETION PROTOCEREBRALE ET EVOLUTION DES OVOCYTES CHEZ *SARCOPHAGA ARGYROSTOMA* (DIPTERE CYCLORRHAPHE)

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Le cerveau imaginal de *Sarcophaga argyrostoma* est doté d'une grande variété de cellules neurosécrétrices dispersées dans différentes régions, le deutocérébron excepté. Au niveau de la *pars intercerebralis*, se situe le groupe le plus important de ces cellules, constitué par une vingtaine d'éléments se colorant à l'azan, à l'hématoxyline chromique de Gomori et à la fuchsine paraldéhyde.

Dans les conditions d'élevage réalisées, *S. argyrostoma*, espèce ovovivipare, présente quatre cycles d'ovogenèse durant la trentaine de jours de sa vie adulte. Dès l'émergence imaginale, les ovocytes amorcent un premier cycle, et, après une croissance très rapide, parviennent à leur taille finale en cinq jours. Emis à l'intérieur de l'utérus, fécondés, leur développement s'achève en quatre jours et les jeunes larves sont expulsées par la mouche âgée de 9 jours.

Le deuxième cycle s'amorce aussitôt après le passage dans l'utérus du lot précédent d'ovocytes, c'est à dire au cinquième jour de la vie de l'imago. La croissance des ovocytes correspondants, d'abord très lente durant les quatre jours de développement intra-utérin des larves du premier cycle, s'accélère fortement après émission de ces dernières. De toute évidence, la présence d'oeufs en développement à l'intérieur de l'utérus inhibe l'évolution des ovocytes de la poussée suivante. La sortie des larves du deuxième cycle s'effectue chez la mouche de 16 jours. Les troisième et quatrième cycles se déroulent de façon similaire.

En somme, la première formation d'ovocytes se singularise par l'absence d'un ralentissement initial de croissance, fait probablement lié à l'état de vacuité de l'utérus.

De tous les éléments neurosécréteurs cérébraux, seules les cellules de la *pars intercerebralis* varient de façon importante et constante en parallèle avec le développement ovarien. Une échelle grossièrement quantitative a été établie, définissant quatre états successifs du neurosécrétat entre l'absence totale de produit dans le péricaryone (état I) et une grande abondance de grains de sécrétion agglomérés en flaques envahissant la totalité du cytoplasme (état 4).

L'évolution de ces cellules neurosécrétrices et de l'ovaire a été étudiée chez des femelles élevées isolément en présence d'un mâle du même âge.

Du premier au cinquième jour de l'ovogenèse initiale, la quantité de neurosécrétat augmente jusqu'à l'état 4, qui se maintient durant les quatre jours d'incubation. Au moment de l'émission des larves, une brusque disparition du neurosécrétat ramène les cellules à l'état I. Il a été déjà indiqué qu'à cet instant se situe l'accélération de croissance du deuxième lot d'ovocytes.

Immédiatement après, la charge des cellules neurosécrétrices de la *pars intercerebralis* manifeste une nouvelle augmentation jusqu'à accession, quatre jours après la parturition, à l'état 4 qui demeure également inchangé au cours de la deuxième incubation. Au terme de celle-ci, rejet des larves, nouvelle décharge de neurosécrétat et accélération de croissance des ovocytes du troisième cycle se manifestent en coincidence. Les troisième et quatrième cycles offrent les mêmes caractéristiques.

Il ressort de ces faits que, chez *S. argyrostoma*, les phénomènes de neurosécrétion au niveau de la *pars intercerebralis* et, d'autre part, l'évolution des ovocytes présentent une corrélation évidente. La décharge du neurosécrétat est suivie de l'accélération de la croissance des ovocytes. Par ailleurs, pendant toute la durée de cette croissance et pendant celle de l'incubation intrautérine, une nouvelle accumulation de neurosécrétat précède la mise en route du cycle ovarien à venir.

Thomsen (1952) avait apporté la première preuve expérimentale d'une action des cellules neurosécrétrices cérébrales médianes de *Calliphora erythrocephala* sur le développement ovarien. Il ne peut être fait état, dans cette brève note, des indications nombreuses concernant les corrélations entre éléments neuro-sécréteurs protocérébraux et fonctionnement ovarien.

Les présents résultats s'apparentent essentiellement aux données de Highnam (1962) qui a montré que, chez *Schistocerca gregaria*, il existe un parallélisme fonctionnel entre les cellules neurosécrétrices de la *pars intercerebralis* et l'évolution des ovocytes.

NEUROSECRETORY CONTROL OF THE DEVELOPMENT OF SEX-ORGANS IN THE WOLF-SPIDER *LYCOSA CHAPERI* (SIMON)

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Post-embryonic development: In male spiders the copulatory apparatus, called the palpal organ, develops during the post-embryonic growth of a spider within the tarsal joint of its gnathal appendage, the pedipalp (1, 2). It is argued that this organ does not develop as a result of hypertrophy of the pretarsus. In 1962 we started studying the development of this organ in the wolf-spider *Lycosa chaperi* (Simon) and were fortunate in coming across a case where the claw does not lose its shape and size up to the final moult. The presence of the claw and the development of the palpal organ is a simultaneous process in this spider. Therefore, the development of the palpal organ in spiders is not due to the hypertrophy of the pretarsus but it is the beginning of a new series of events in the fate of the apical epidermal cells of the tarsus. While the phylogenetic development and origin of the palpal organ in spiders has an evolutionary bearing, its ontogenetic development, is probably under an intrinsic control.

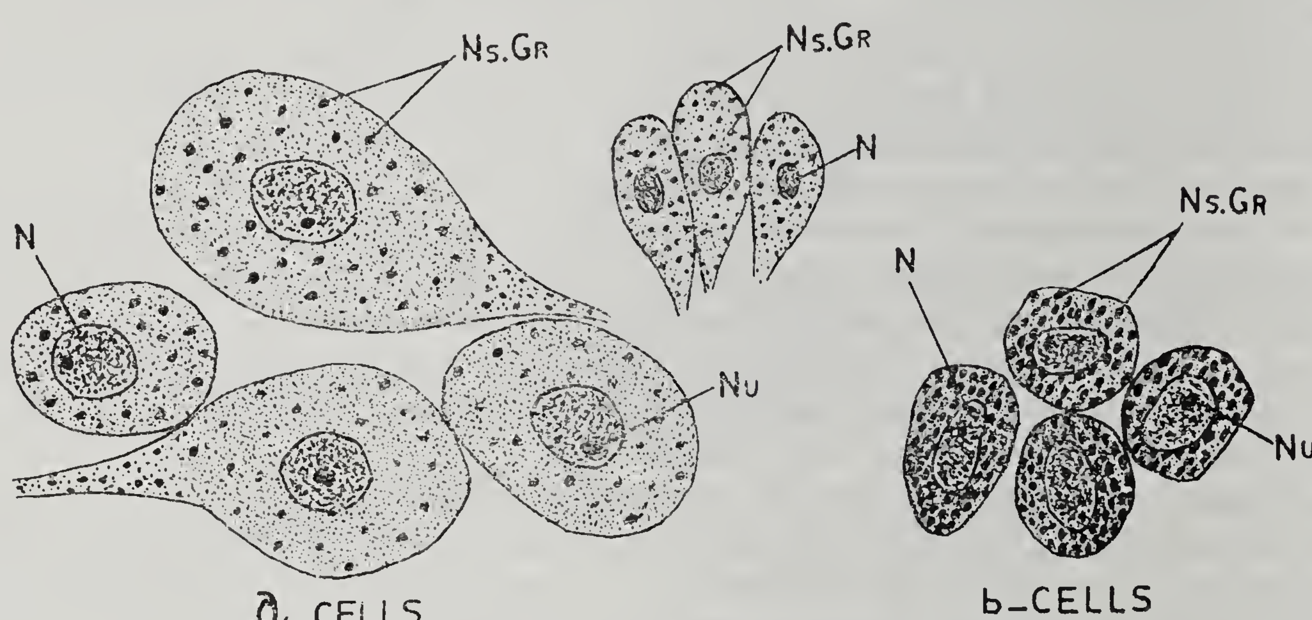

Fig. 1. Neurosecretory cells of *Lycosa chaperi*

The brain of Lycosa chaperi. The nervous system was studied in some detail with a view to locating the neurosecretory centres in the brain and the sub-oesophageal ganglionic mass. The brain is a syncerebrum constituted by a protocerebrum, a greatly reduced tritocerebrum represented by the stomodaeal bridge, and the cheliceral ganglia (3, 4).

It was observed that the nervous system in *Lycosa* is not associated with any endocrine organ such as the corpora allata and corpora cardiaca of insects. The only source of endocrine secretions associated with the nervous system are the neurosecretory cells which have been located and studied in the present species. The gonadal hormones which are known to control the development of the secondary sexual characters in some animals have so far not been studied in any spider. The development of the gonads themselves may be under an influence of the secretion of the neurosecretory cells as in certain insects.

The neurosecretory cells were studied in both male and female adult spiders and in 8th and 9th male instars when the palpal organ also develops. The neurosecretory cells are located in the posterior region of the brain and along the outer margins of the sub-oesophageal nerve mass. Two types of cells have been observed, (1) a-type and (2) b-type. The a-type cells are larger occurring only in bunches and b-type cells are smaller occurring singly. Both types of cells were seen in various stages of secretion.

a-type cells are larger in size, glandular in appearance with a spongy cytoplasm and with a nucleus of an irregular outline. They contain a large number of deeply staining granules.

b-type cells are smaller in size, with a more compact cytoplasm and with a rounded nucleus. The deeply staining granules cover almost the entire cytoplasm.

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PHYLOGENETIC CONSIDERATIONS ON THE JUVENILE HORMONE AND OTHER MORPHOGENETICALLY ACTIVE SUBSTANCES IN INSECTS

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Information on the juvenile hormone has greatly increased in recent years. However, many questions remain to be answered and controversy continues over the character and mode of action of the corpora allata secretion. Nevertheless the available data allow the first fairly

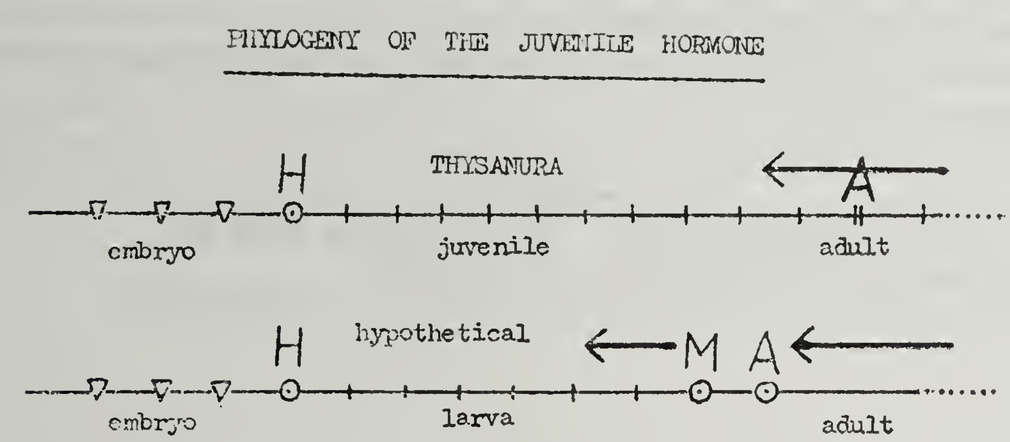

Fig. 1. Phylogeny of the juvenile hormone. Thick arrow—period of activity of JH; H—the moment of hatching; M—the beginning of metamorphosis; A—the adult ecdysis; S—subimaginal ecdysis; lu—larvula.

clear preliminary conclusions on the evolution of this most important factor in the phylogeny of pterygote insects.

The present considerations are based on the following suppositions not yet generally agreed:

(*a*) There is only one corpus allatum hormone, the juvenile hormone (JH), responsible for all the observed effects of allatectomy and reimplantation of the gland (3).

(*b*) The morphogenetic effects of cecropia extract and of extracts obtained from various other organisms are different from those of the corpus allatum hormone. They correspond to those of the morphogenetically active chemicals such as some of the both unsaturated and saturated fatty acids, farnesol derivatives and polyisoprenoid compounds (2).

(*c*) There is a close relation between the metamorphosis hormone system of insects and the hypothalamo-hypophyse system of vertebrates, the juvenile hormone corresponding to the somatotropin of adenohypophysis. This relation is less than true homology but more than a mere analogy. It corresponds to the relation between the nervous system in invertebrates and that in vertebrates (3).

Very primitive corpora allata appear in some of the highest Apterygota (Lepismatidae, Japygidae). There are no morphogenetical effects of JH here, but the hormone seems to be concerned with the development of ovaries (1).

It is concluded that the original function of the JH is the gonadotropic one. Its morphogenetical activity developed in connection with its increasing production favoured by natural selection only subsequently in phylogeny of insects. In this way the larval period of isometric growth and the resulting metamorphosis originated as the first steps in the evolution of Pterygota. The further intensification of the JH production and the spreading of the period of its activity into earlier and earlier stages of ontogeny due to its high selective value led to the evolution of Holometabola afterwards on the principle of desembryonisation as shown by the Berlese-Jeshikov theory (1).

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PHYSIOLOGY AND BIOCHEMISTRY—CONTRIBUTED PAPERS

EXPERIMENTAL RESEARCHES ON MALPIGHIAN TUBULES OF TENEBRIONID BEETLES

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Ramsay (8) reached the conclusion that urine formation in insects is due to three mechanisms, diffusion, secretion and absorption, whereas in vertebrates we are confronted with filtration, secretion and absorption. Mazzi and Baccetti (4, 5, 6) localised the site of the enzymes of malpighian tubules which most probably intervene in the cellular work of secretion or absorption (specific and aspecific phosphatases, succin-dehydrogenasis, etc.); other work has been done on *Galleria mellonella* (7) and *Gryllus domesticus* (1).

Some drugs or chemicals which have a diuretic action on vertebrates act in the same way in insects (3), thus pointing to a similar—if not identical—physiology of vertebrate nephron and insect malpighian tubule. Some of these substances probably function through inhibition of -SH groups of succin-dehydrogenasis or eventually of carbo-anhydrasis. The same action has been successively demonstrated in other species of Coleoptera or in other stages of the beetle *Tenebrio molitor*. As far as the secretory function of the malpighian tubules is concerned, I have employed a number of substances which generally are actively secreted in the vertebrate kidney, such as inulin, penicillin, p-amino hippuric acid and diodone. The results are shown in fig. 1. We can deduce that the malpighian tubules of insects behave in a rather similar way compared with the vertebrate nephron, but while penicillin, diodone and p-amino hippuric acid are eliminated quickly in the first days and later slowly, inulin is eliminated very regularly

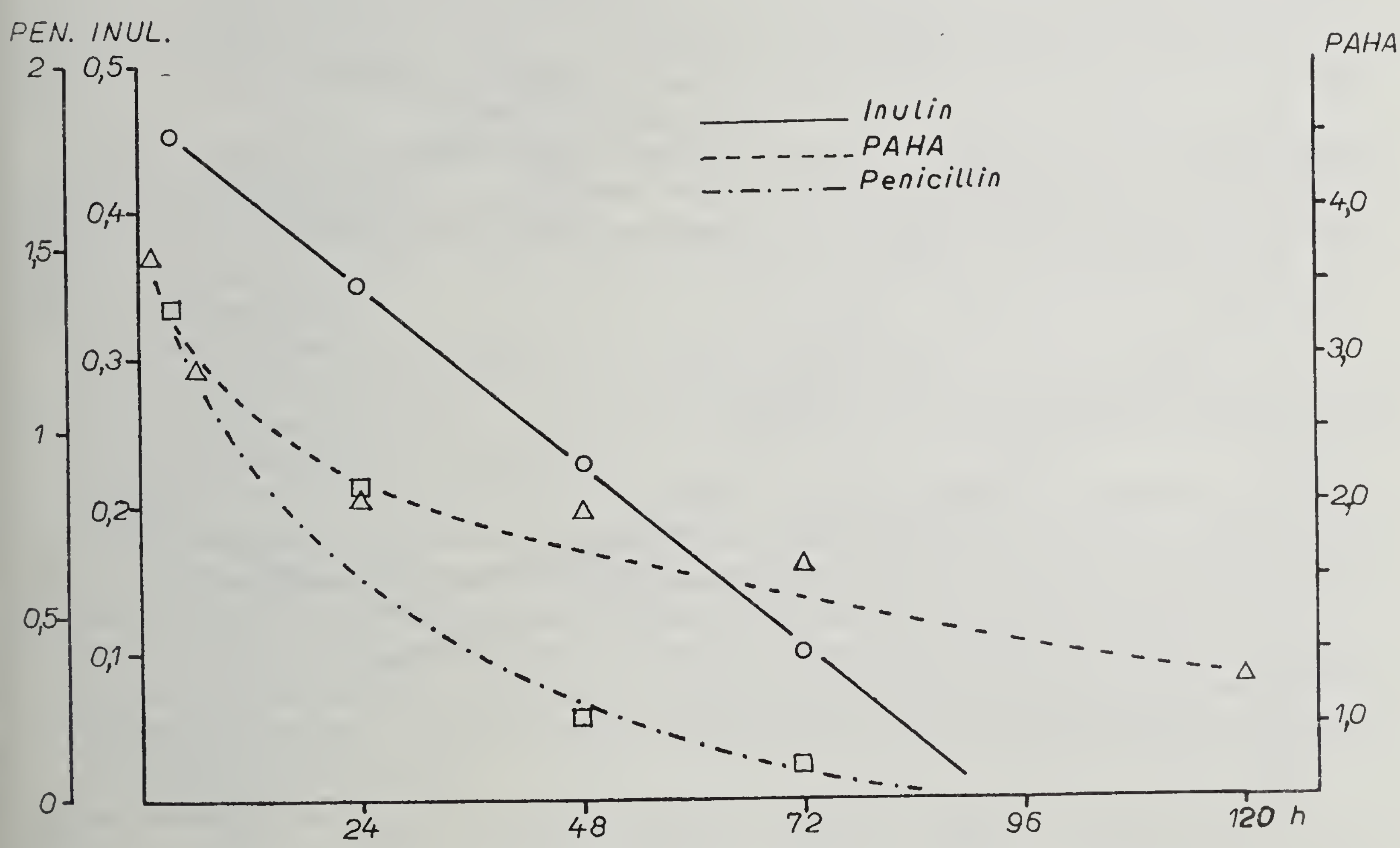

Fig. 1. Results of experiments on malpighian tubules of *T. molitor*.

over the entire period. It would appear that while the former substances diffuse passively, the latter is very probably actively secreted. In order to see whether the elimination of inulin is really completely active, I have examined the elimination of this substance in insects which had been previously poisoned with DNP, papaverine or rotenone, and the results show a clear effect of poisoning on elimination (fig. 2). At the same time inulin excretion is influenced by probenecid, the well known effect of which is the blockage of tubular excretion in vertebrates.

As far as the exact site of elimination is concerned, some experiments with radio-penicillin show that this substance is eliminated quickly in the first day, when it appears in the intestine and only in the most proximal portion of the malpighian tubules and then very slowly. The use of aureomycin gives very similar results.

Lastly I have examined the action in insects of some substances which in vertebrates behave as renal poisons, uranyl nitrate, potassium bichromate, mercuric chloride, lead acetate, etc., and are often associated with renal cell damage. The results point to an analogy of effects in insects compared with vertebrates (2, 9).

We can conclude from this that the malpighian tubules of insects are constructed and function very much as the vertebrate kidney.

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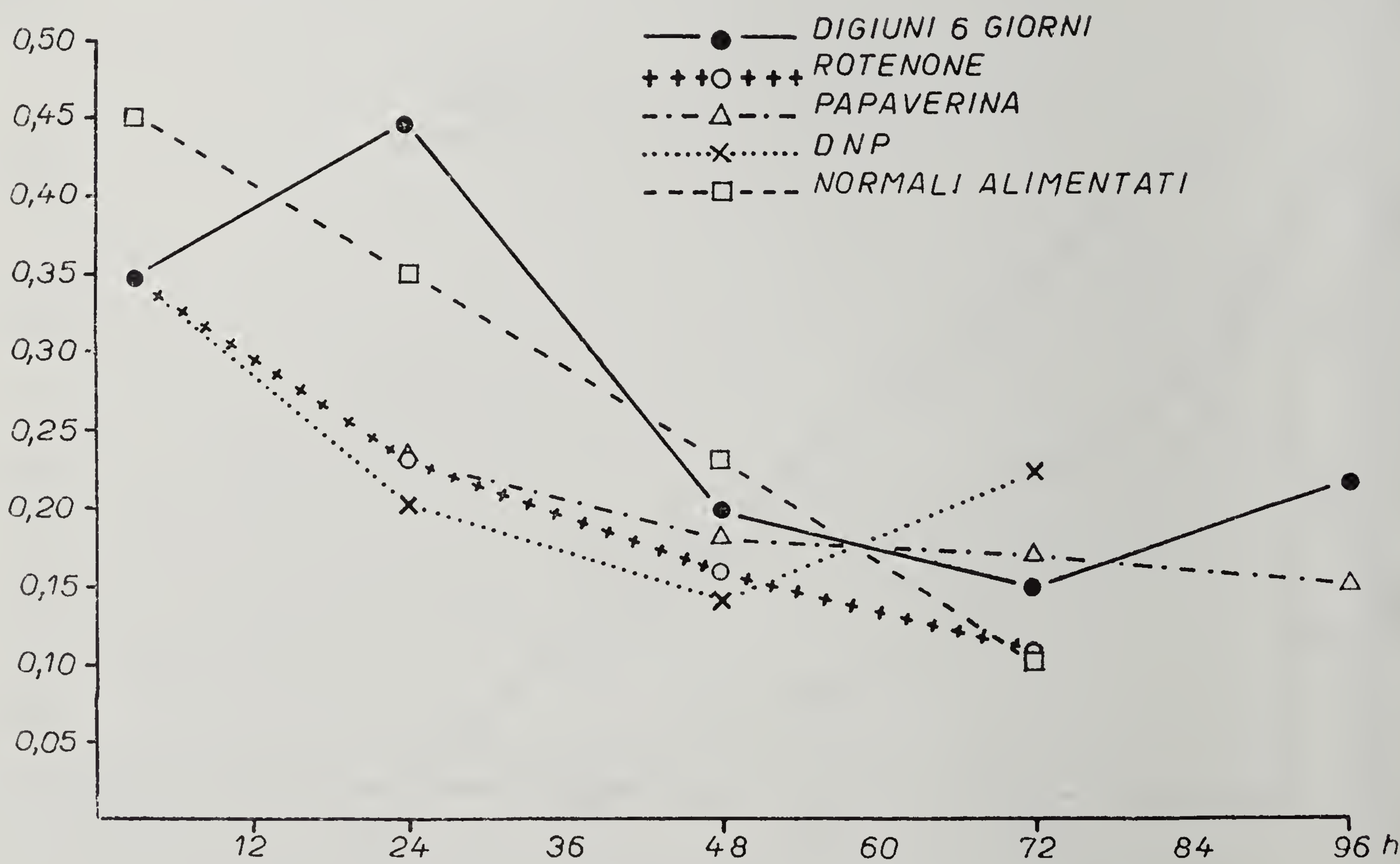

Fig. 2. Results of experiments on malpighian tubules of *T. molitor*.

CONTRIBUTION A L'ETUDE DU CATABOLISME AZOTE DES MYRIAPODES (CHILOPODES ET DIPLOPODES)

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En 1890, Marchal, à la suite d'un certain nombre d'auteurs, a considéré comme générale l'excrétion d'acide urique chez les Myriapodes.

Nous avons cherché à savoir si cet acide urique est réellement le seul catabolite terminal chez tous les Myriapodes, et s'il n'est pas, chez diverses espèces, au moins partiellement dégradé par les enzymes uricolytiques ainsi que c'est le cas chez de nombreux Insectes.

Notre travail a porté tout d'abord sur l'uricase: nous avons fait agir à température et temps déterminés, des poudres, (obtenues à partir des sujets à étudier par dessiccation et broyage) sur une solution tamponnée d'urate de lithium, en nous plaçant dans les conditions considérées par les auteurs comme les plus favorables pour l'étude "in vitro" de l'uricase (en tampon acide borique soude de pH 9, 2-9, 3).

Par spectrophotométrie différentielle nous avons dosé, en fin d'expérience, l'acide urique non détruit par l'enzyme. Chez toutes les espèces ainsi étudiées, nous avons observé la disparition d'une quantité variable d'acide urique, correspondant à une certaine action uricasique.

Nous interprétons cependant ces résultats avec prudence, car ils sont obtenus dans des conditions expérimentales très différentes au point de vue pH et composition ionique de celles du milieu naturel. De plus, nous n'avons jamais pu mettre en évidence chez nos sujets le catabolite correspondant: l'allantoïne.

Les autres enzymes de l'uricolyse: allantoïnase, allantoïcase ont été également recherchées, ainsi que les catabolites dont elles favorisent la formation: acide allantoïque, acide glyoxylique. Les résultats ont toujours été négatifs. L'uréase semble exister chez tous les Diplopodes, par contre, l'urée n'a pu être mise en évidence de façon appréciable.

Ensuite, nous avons recherché l'acide urique et en accord avec les auteurs précédents, nous avons constaté sa présence générale dans les tissus, les excreta et l'hémolymphe de nos espèces. Par spectrophotométrie différentielle, nous en avons évalué la teneur dans les tissus et dans les excreta. Nous avons retrouvé cet acide urique par chromatographie sur papier: les Rf des taches obtenues à partir des hémolymphes semblent indiquer le plus souvent, la présence d'urate de sodium, et peut-être celle d'urate d'ammonium chez *Cylindroiulus londinensis* C.L.K.

Enfin, tous les Myriapodes étudiés libèrent et éliminent aussi de l'ammoniaque, même les Chilopodes qui sont dépourvus d'uréase. Les recherches en cours permetteront de préciser l'importance de ce dégagement d'ammoniaque, qui, aux observations préliminaires, nous a paru très abondant. Alors, nous pourrons comparer quantitativement l'excrétion ammoniacale à l'excrétion urique.

Ces observations, nous suggérent les conclusions ci-après:

1° La présence de l'uricolyse in vivo n'est pas prouvée avec une certitude absolue; si elle existe, elle n'est que limitée: une partie de l'acide urique y échappe et est éliminée dans les excreta sans subir de dégradation.

2° L'absence de la chaine uricolytique complète, nous fait considérer l'ammoniaque comme ne pouvant provenir que du catabolisme protidique; cette ammoniaque se forme peut-être par la voie de l'urée chez les Diplopodes qui possédent de l'uréase; chez les autres, on peut admettre l'hypothèse qu'elle provient de la désamination des acides aminés.

3° Les teneurs en acide urique semblent parfois trop importantes pour pouvoir être expliquées par le seul catabolisme purique, et on peut se demander s'il n'existe pas alors chez les Myriapodes, comme chez les Insectes, une formation synthétique d'acide urique à partir de catabolites protidiques.

LE PROBLEME DE L'ACIDE URIQUE CHEZ LES ARTHROPODES ANTENNATES

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Chez de nombreux Insectes, l'acide urique n'est pas un catabolite terminal, étant lui-meme dégradé en allantoïne par l'enzyme uricase. Grâce à la caractérisation et au dosage de l'allantoïne ainsi formée, l'uricase a été mise en évidence chez des Hétérométaboles (Hétéroptères) et chez de nombreux Holométaboles (1).

Actuellement, l'étude de l'uricase est conduite par spectrophotométrie différentielle, grace au pouvoir absorbant de l'acide urique en solution vers 290 mμ. Cette méthode a permis de constater que l'uricase des Insectes possède sa plus grande activité *in vitro* à pH 9,3 en tampon borate-soude, et à des températures se situant, selon les espèces, soit aux environs de 28°C, soit aux environs de 38°C. Grâce à cette méthode, nous avons repris la recherche de l'uricase chez les Orthoptéroïdes, qui précédemment nous avaient semblé en être dépourvus. Les expériences ont été conduites simultanément à 28°C et à 38°C à la fois en tampon phosphate de pH 7.4 et en tampon borate de pH 9,3. Les résultats, souvent positifs, doivent être interprétés avec prudence. Le tampon borate à pH 9,3 détermine des conditions très différentes de celles du milieu naturel. Le tampon phosphate à pH 7,4 en est plus proche. On pourra admettre une uricolyse partielle chez ceux des Insectes étudiés qui contiennent ou éliminent de petites quantités d'allantoïne: *Blatta orientalis, Periplaneta americana, Acheta domestica, Locusta migratoria, Schistocerca gregaria.*

Des expériences semblables ont permis de mettre en évidence une uricase notable chez le Coléoptère Buprestide *Chrysobothris affinis*, une uricase faible chez le Ténébrionide *Tenebrio molitor.* Ces faits étant en accord avec l'excrétion d'allantoïne, l'uricolyse semble prouvée.

Nous sommes beaucoup plus réservés devant les résultats obtenus en présence de divers Insectes aquatiques; larves d'*Aeschna*, de *Somatochlora*, de *Limnophilus*, de *Chironomus*, imagos de *Corixa punctata*: chez ces sujets nous n'avons pu mettre en évidence l'allantoïne; on peut donc se demander s'il y a bien uricolyse *in vivo.*

L'allantoïne est le catabolite terminal chez les Hétéroptères, les Muscides à larves créophages, les Coléoptères Buprestides. Elle est transformée en acide allantoïque par l'allantoïnase chez de nombreux Holométaboles et chez quelques Polynéoptères. Mais, le plus souvent, l'uricolyse est partielle; acide urique, allantoïne et acide allantoïque sont retrouvés ensemble dans les excreta.

L'acide allantoïque est scindé par l'allantoïcase en acide glyoxylique et en urée chez un très petit nombre d'espèces (1).

En outre, une excrétion très importante d'ammoniaque est connue chez les larves créophages de Muscides, et chez des Insectes aquatiques. Nous avons nous-même observé cette excrétion chez les larves d'*Ephemera vulgata*, d'*Anax*, de *Somatochlora metallica*, de *Calopteryx splendens*, de *Dytiscus semisulcatus*, de *Glyphotaelius pellucidus*, de *Stenophylax rotundipennis, de Limnophilus lunatus*, de *Lasiodiamesa* et de *Chironomus*, et les imagos de *Nepa rubra* et de *Corixa punctata.*

Une uréase (très peu active *in vitro*) peut permettre la formation d'ammoniaque à partir de l'urée chez quelques espèces: Lépidoptères Piérides, larves de *Chironomus*, de *Glyphotaelius.* L'ammoniaque peut aussi se former en petites quantités lors de la désamination des bases puriques. On considère qu'elle provient pour la majeure partie de la désamination directe des acides aminés (2). En aucun cas, elle ne dérive de l'acide urique.

La formation et l'élimination de quantités importantes d'ammoniaque chez certains insectes aquatiques conduisent à la conclusion que catabolisme purique et catabolisme protidique restent au moins partiellement indépendants.

Les autres Antennates semblent devoir être rapprochés des Insectes aquatiques. Les Crustacés, en effet excrètent à la fois de l'acide urique et de l'ammoniaque; mais l'uricolyse y est peu importante ou nulle (3). Des recherches en cours annoncent le même schéma chez les Myriapodes (4).

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EFFECT OF AGE ON HUMIDITY RELATIONS IN ADULTS OF *TRIBOLIUM CONFUSUM* DUVAL

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Adult beetles were used to eliminate complications brought on by life-cycle changes and maintained individually to eliminate effects of reproduction and crowding. Beetles were weighed in groups of 30 to increase accuracy and separated in small containers during treatments. Age was carefully controlled by making up all groups from animals that had emerged within two days of each other. Some groups were picked out at random, weighed, dried and weighed again to give the initial water and dry-matter contents of the experimentals. The latter were weighed, exposed to a controlled humidity at $25 \pm 0{\cdot}5$°C for the required time, weighed, dried, and weighed again. Weight loss in groups of 30 beetles was measured after starvation for six days, and the dry matter and losses derived from initial and final dry-weight figures, as above.

Weight was found to remain essentially constant over a three-month period except for an initial drop in the first few days. In contrast, water content decreased and dry matter increased markedly for the first two months, presumably because of fat accumulation and reduced water. After this, the two components tended to approach each other as the beetles began to go into senescence and to lose lipids. There is no reason known to us as yet for the maintenance of a constant weight, unless it is the obvious one that they are normally at maximum volume and cannot increase their mass because of an inelastic cuticle. Thus as fat increased, water would have to decrease, and vice versa. With proper regulation, the slow changes we observed would leave the blood essentially unchanged in composition and the cellular environment would be quite stable.

Young beetles (1-2 weeks) lost weight faster in all humidities than older (2 months) ones, both living and dead. In the latter, it is due to water loss, but in living animals, the difference was found to be due to losses in dry matter. There is water loss, but it is the same in both groups, showing regulation in the face of differences in age, metabolic rates, and reproductive state. The fact that there was an age difference in dead animals supports this thesis. The mechanism for such regulation is unknown to us, but it may be based on the spiracular system. The ability to regulate water loss might well be one of the major factors in the success of these small animals.

The age differences in water and dry-matter content and in weight loss will explain much of the variation found in these animals by earlier workers who took their samples from mass cultures without controlling their ages. The present study and other work to be reported elsewhere show that minor differences, lost in averaged replicates, are exceedingly important in the determination of the physiology of water balance in these beetles.

COMPARATIVE STUDIES ON OXYGEN CONSUMPTION IN THE ALBINO AND NORMAL STRAINS OF *SCHISTOCERCA GREGARIA* BRED UNDER CROWDED AND ISOLATED CONDITIONS

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O_2-consumption was measured in the Warburg apparatus at 33°C, once in each nymphal instar one day after the moult, and in adults 1, 5, 11 and 21 days after fledging, using resting locusts which had been fasting for one day. Males and females of both strains under both breeding conditions were investigated. Crowded locusts uniformly went through 5 moults. In isolation some moulted 5, and some 6 times and each of these types, altogether 1,599 individuals, were investigated.

The equation $Y = aX^b$ ($Y = O_2$-consumption in μl./hr., X = fresh body weight in grammes, a and b = constants) was found to correlate well with the average experimental results, obtained for successive nymphal instars and for day-old adults of both sexes.

The following equations were found to fit the O_2-consumption—

Albino strain:
- crowded locusts, 5 moults: $Y = 706{\cdot}3X^{0{\cdot}936}$
- isolated locusts, 5 moults: $Y = 660{\cdot}7X^{0{\cdot}951}$
- isolated locusts, 6 moults: $Y = 648{\cdot}6X^{0{\cdot}953}$

Normal strain:
- crowded locusts, 5 moults: $Y = 680{\cdot}8X^{0{\cdot}942}$
- isolated locusts, 5 moults: $Y = 597{\cdot}0X^{0{\cdot}935}$
- isolated locusts, 6 moults: $Y = 616{\cdot}6X^{0{\cdot}936}$

However, these equations do not express the changes of O_2-consumption during imaginal development, probably because the metabolic changes are so marked in adults of different ages that they partially obscure the influences of the changes in body weight on O_2-consumption.

The values of b in the above equations show little changes for different strains and breeding conditions. The same value (about 0·94) probably applies to all cases. Thus, it seems that the O_2-consumption of locusts defies the "surface law". This conclusion is supported by calculating values of b, using data found in the literature (1 and 2).

The numerical values of a are in both strains higher for crowded locusts. Thus, according to the respiratory equations, their O_2-consumption is higher than that of isolated locusts. In this way an efficacious method for comparing O_2-consumption of locusts undergoing 5 and 6 moults was found.

By expressing O_2-consumption on a fresh body weight basis (in μl./hr. mg.), the following results were obtained:

1. From the 4th instar onward females showed slightly lower (less than 5%) O_2-consumption than the males, which could be accounted for, by the differences in body weight, as the former are heavier than the latter. As the differences were very small they are neglected below.
2. Crowded hoppers of either strain showed a higher O_2-consumption than isolated ones (see figs. 1 and 2).
3. Differences in O_2-consumption were apparently insignificant between crowded and isolated locusts, for adults aged 1, 5 and 11 days. In contrast, 21 day old adults consumed more oxygen under crowded conditions.
4. In crowded locusts a U-shaped respiratory curve was obtained through the imaginal development of either strain.

Since in both strains changing of the breeding conditions resulted in similar changes in the O_2-consumption, it was concluded that the presence of melanin—which occurs in the crowded (gregarious) hoppers of the normal strain—is not responsible for the differences in the basic O_2-consumption between gregarious and solitary locusts.

Figure 1

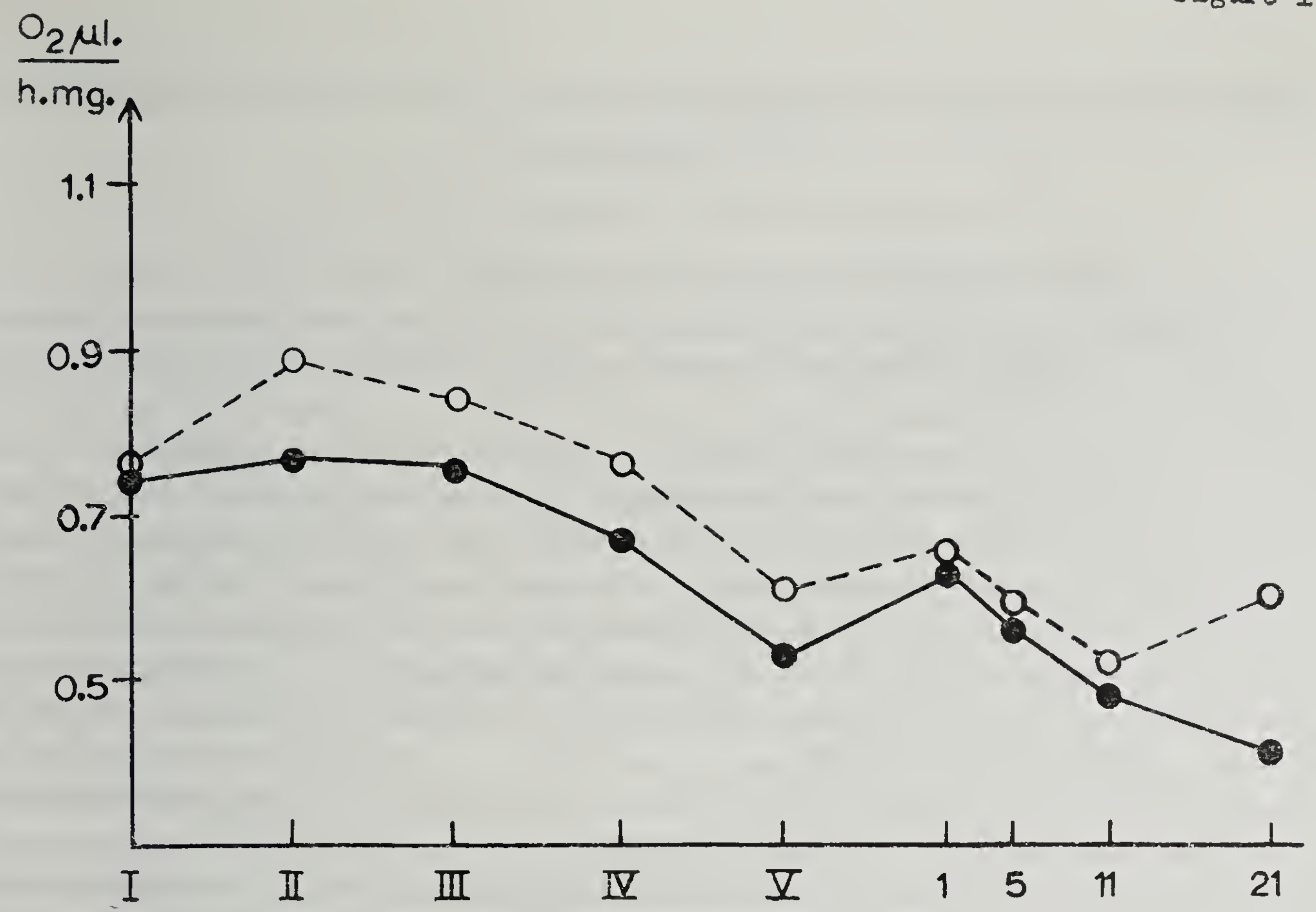
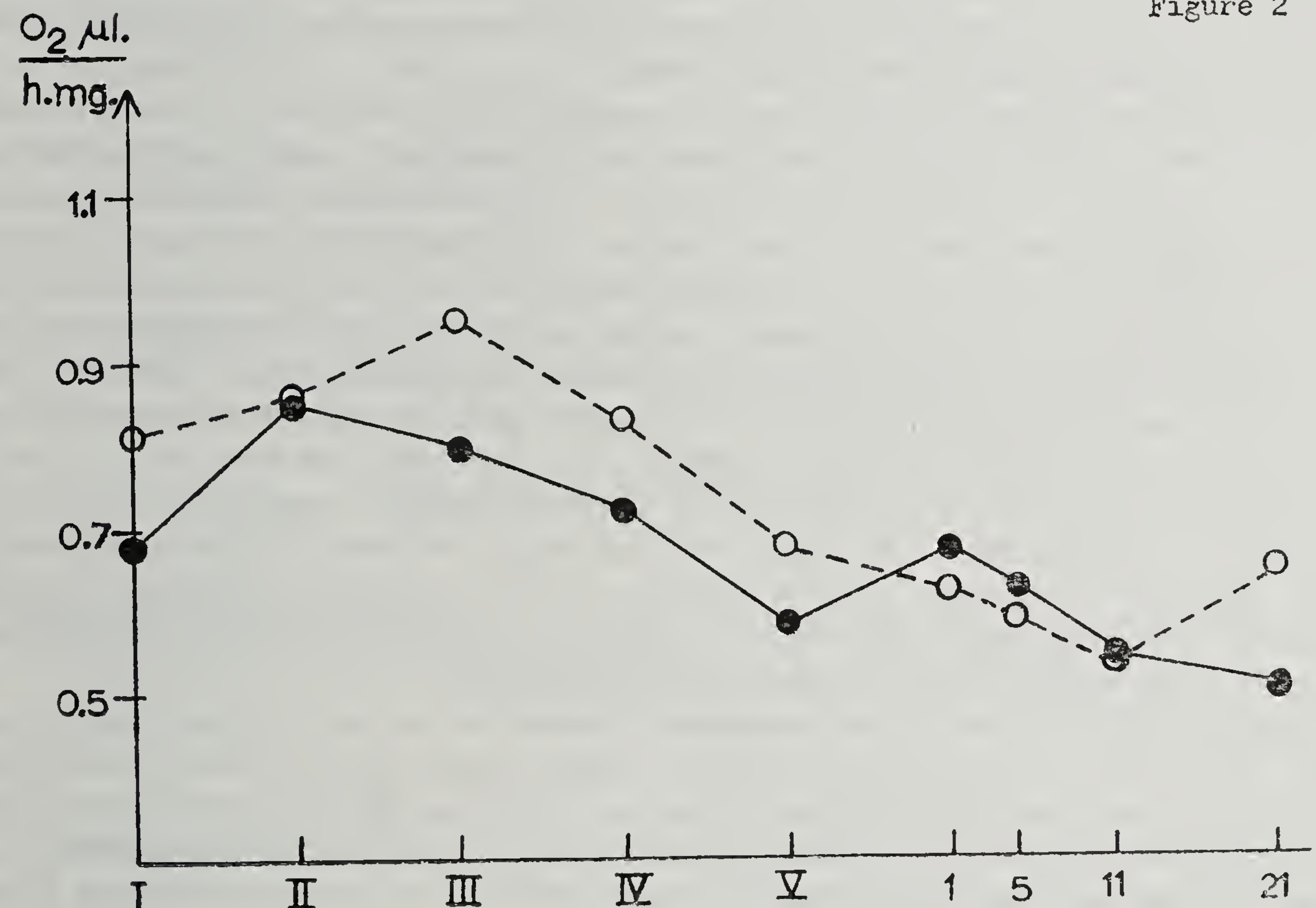


Figure 2



FIGS. 1 AND 2. Average O_2-consumption (expressed in µl./hr.mg.) in the normal and albino strain respectively. Dots connected by continuous line show results obtained for isolated locusts (only those which underwent 5 moults are included), circles connected by broken line show results obtained for crowded locusts. Roman numbers show nymphal instars, arabic numbers show age of adults in days after fledging.

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TUBE-BUILDING BY MACHAEROTID NYMPHS (HOMOPTERA)

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Machaerotid nymphs construct conical shaped dwelling tubes on the stems of their host plants. The following species have been studied: *Chaetophyes compacta* Walker and *Pectinariophyes stalii* Spångberg (Australia), *Makiptyelus dimorphus* Maki (Taiwan), *Machaerota coronata* Maa (Hong Kong).

The dwelling tubes are composed of both inorganic and organic materials. Treatment with dilute mineral acids removes approximately 85% of the total weight; this percentage is presumably mainly inorganic material. In this removable material, carbonate, phosphate, calcium and magnesium have been detected. A preliminary analysis of the organic constituents has been made. Amino acids, identified by chromatography in hydrolysates of "demineralised" dwelling tubes, have identical patterns in 2 species investigated. A preliminary analysis of sugars again shows identical patterns in 3 species and suggests the presence of a complex polysaccharide, possibly a mucocomplex.

In teased portions of "demineralised" tubes, microscopic fibrils are evident and appear to form a meshwork embedded in an organic matrix.

The dwelling tubes are filled with a colourless fluid within which the nymphs are normally submerged. This fluid is excreted by the nymphs via the anus. It contains white or colourless granules and fibrils identical with those seen in teased tubes. During periods of tube-building the abdominal tip of a nymph makes characteristic movements about the lip of the tube whilst pouring fluid from the anus along the tube lip.

The gut of machaerotid nymphs has the typical homopteran filter chamber arrangement. The midgut has a white segment containing cells loaded with white or colourless granules which are composed, at least in part, of calcium and phosphate. From time to time these granules are liberated and pass down the hindgut. They appear to be identical to those found in the fluid filling the dwelling tubes and probably give rise to the calcium and phosphate found in the dwelling tubes. Four Malpighian tubules are present, each divisible into 2 segments. The proximal segment is divisible into a granule zone and a fibril zone. The cells of the fibril zone contain large numbers of fibrils. The fibrils of the 4 species investigated differ in size. A preliminary histochemical analysis suggests that they are composed of a mucocomplex. They selectively bind alcian blue, iron and mucicarmine, yield γ metachromasia with toluidine blue and are P.A.S. negative. Extrusion of fibrils occurs at intervals when tube-building is in progress and nymphs dissected at such times have fibrils within the lumina of their hindguts. Thus the fibril zone appears to be the site of origin of the fibril network in the dwelling tubes and may account for the sugars found in tube hydrolysates.

The fibrils of all 4 species are arranged in stacks within the cell and there is a general tendency for them to be orientated radially with respect to the tubule. After extrusion terminates the fibril zone lumen is seen to be very wide and fibrils are still present within the cells. A fibril zone has never been observed which did not contain abundant fibrils. It would thus appear that the process of extrusion never proceeds to the point at which the cells are completely emptied of their fibril content.

QUANTITATIVE STUDIES ON THE HEMOCYTES OF *RHODNIUS PROLIXUS* STÅL (HEMIPTERA)

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Using phase contrast microscopy, prohemocytes, plasmatocytes, granular hemocytes, and oenocytoids can be readily identified in fresh, thin, wet, coverslipped whole mounts of hemolymph from unfixed *Rhodnius*. These cells have been referred to by Wigglesworth as proleucocytes, amoebocytes, oenocytoids, and large non-granular cells, respectively. Differential counts were made throughout the fourth and fifth stages and for the first two weeks of adult life. Circulating plasmatocytes were measured daily in unfixed wet films throughout the fifth stadium. Because of the great inherent variability in size of these cells, the only statistically significant change was a general decrease in their length during the stadium. Usually 90% or more of the unfixed circulating plasmatocytes vacuolate *in vitro* throughout the life span of *Rhodnius*, and the number and size of these vacuoles could not be correlated with secretion of the moulting hormones. Relative numbers of circulating hemocytes have been made each day throughout the fifth stadium in conjunction with semi-quantitative calculations of the hemolymph volume so that the number of circulating hemocytes in the entire insect could be extrapolated. The hemolymph volume greatly changes in relation to ecdysis and nymphal feeding. Shortly after ecydsis, the hemolymph volume is elevated and the number of circulating cells enormously increased, and then the volume of fluid and the number of circulating cells greatly decrease in the unfed insect. Within about one hour after fifth stage nymphs take a blood meal, the hemolymph volume and the number of circulating cells increase and remain high for the first half of the stadium. When the new cuticle is being formed during the latter half of the stadium, the hemolymph volume is strikingly lowered and the number of circulating hemocytes is decreased.

The cyclic changes in the hemolymph volume and the number of circulating hemocytes in the entire insect are in part probably controlled by hormones. Presumably, hormones cause the hemocytes to adhere to or become released from tissue surfaces. The great changes in the number of circulating hemocytes cannot be correlated with divisions of hemocytes, or with the destruction of cells through phagocytosis, or with lysis of circulating cells.

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ELECTRICAL RESPONSES TO RADIATION IN THE EYE OF THE COCKROACH *BLABERUS GIGANTEUS* (DICTYOPTERA)

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Electroretinograms (ERGs) have been recorded from the compound eyes of cockroaches by means of electrodes inserted under the corneal layer. In light adapted specimens, the response to brief bursts of X-rays was approximately 5 per cent of that found in fully dark adapted insects. After two hours of dark adaptation, ERGs measuring 500 microvolts in amplitude appeared at dose rates of 190R/min. Using a pulsed beam of X-rays, it has been shown that the amplitude of the ERG is dependent on total dose per pulse and independent of dose rate over the range studied. The eyes react to very low doses of X-rays, and a response of 6 microvolts occurred at a total dose of 0·09 mR.

CONTROL OF FLASHING IN FIREFLIES

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In lampyrid fireflies the lantern consists of many thousand small photocytes, yet in some species the animal is able to synchronise their activity within periods as short of 0·1 sec (100 msec.). This control was studied by electrical stimulation of central and peripheral nerves, with the resulting light-production being detected with a photomultiplier tube and displayed on an oscilloscope screen; and by recording action potentials from central and peripheral nerve.

Electrical stimulation can elicit flashes kinetically indistinguishable from the normal spontaneous flashes. Moderate stimulation, even with electrodes on peripheral nerve in luminous tissue, induces responses of remarkably long latency: about 70 msec at 25° in *Photuris pennsylvanica* and up to 200 msec in some species of *Photinus*. Stimulus strength and duration for threshold response show a parabola-like resultant curve as in muscle. Facilitation of response with repetitive stimulation is very marked, and records resembling summation, treppe and tetany in striated muscle can be obtained. Adaptation and fatigue can be demonstrated. Statistical analysis of flash intensity and frequency in a long series of spontaneous flashes indicates that flash intensity reflects degree of neural facilitation rather than photogenic substrate concentration.

Central conduction velocity is in the range 15-50 cm/sec. Spontaneous flashing is abolished by decapitation or cord section. The central nervous system is also involved in the production of compound flashes, in "after-discharge" luminescence following strong stimulation, in comatose behavior (probably associated with the diurnal cycle of luminous activity), and in the normal flash responses in the mating signal system. Central inhibition of both spontaneous and induced flashing can be induced by stimulating with electrodes in one eye.

Characteristic 2-7 spike volleys preceding each spontaneous flash are detectable in the posterior cord in *Photuris*. The same volleys, free of most extraneous "noise", appear about 5 msec later in peripheral nerve in lantern tissue, preceding both spontaneous and induced flashes. Volley-flash latency is about 70 msec. Though the electrodes are presumably receiving from several nerves it is possible to demonstrate statistical association of flash intensity with both volley frequency and spike frequency.

By using strong stimulation or minute pieces of lantern tissue it is possible to induce flashes with a latency of only about 18 msec as compared with the usual 70. Under proper conditions both this new "quick flash" and the usual "slow flash" can be elicited in sequence by a single stimulus. The quick flash resembles the slow in contour and kinetics, in showing strength-duration relations for threshold, in apparently originating in the same tissue, and in showing facilitation, summation, fatigue, etc. It differs from the slow flash in latency, in having a higher frequency compliance and higher threshold, and in showing scarcely any latency change with temperature (Q_{10} 1·4 or lower) as compared with the slow flash (Q_{10} 2·0 or higher).

We believe that slow flash and quick flash represent the same effector event, excited by different processes or pathways. This view is supported by the fact that denervated lanterns are excitable for both slow and quick flashes for about 24 hours, but thereafter (the peripheral nerves having by then degenerated) only for the quick flash. Hence quick flash excitation can be viewed as a by-passing, by intense stimulation, of part of the normal excitation pathway. It seems likely that the total post-synaptic latency of about 70 msec comprises a small peripheral conduction delay plus a considerable end-organ excitation delay (total about 50 msec), and about 18 msec of photocyte excitation delay.

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OPTICS OF THE COMPOUND EYE IN RELATION TO INCREASE IN SIZE

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The present paper continues work by the authors (1, 5) and considers the changes in the eye when the separation (usually equivalent to the diameter) of the ommatidia changes. Suppose (*a*) that the wavelength for which the eye is most sensitive does not change; indeed insect eyes show general agreement in their peak wavelength sensitivity (3); and (*b*) that the same number of successive diffraction images is contained in the region distal to the basement membrane; now if the separation increases from b to b′ and the region over which diffraction images are formed increases from d to d′, then $\frac{b^2}{d} = \frac{b'^2}{d'}$, (4). "b" is measured with an eyepiece micrometer. The focal point of the ommatidial lenses is observed using a minute bright object beneath the microscope stage and "f" is measured from the eye surface with the fine adjustment micrometer. Since the focus lies as the end of the crystalline cone, the final value for "f" was the mean of the optical value and the length of the cones measured on sections. The depth of the basement membrane is measured on Bouin fixed gelatine frozen sections checked against fresh frozen eyes. By deducting "f" from this value we get the distance "d" over which diffraction is occurring.

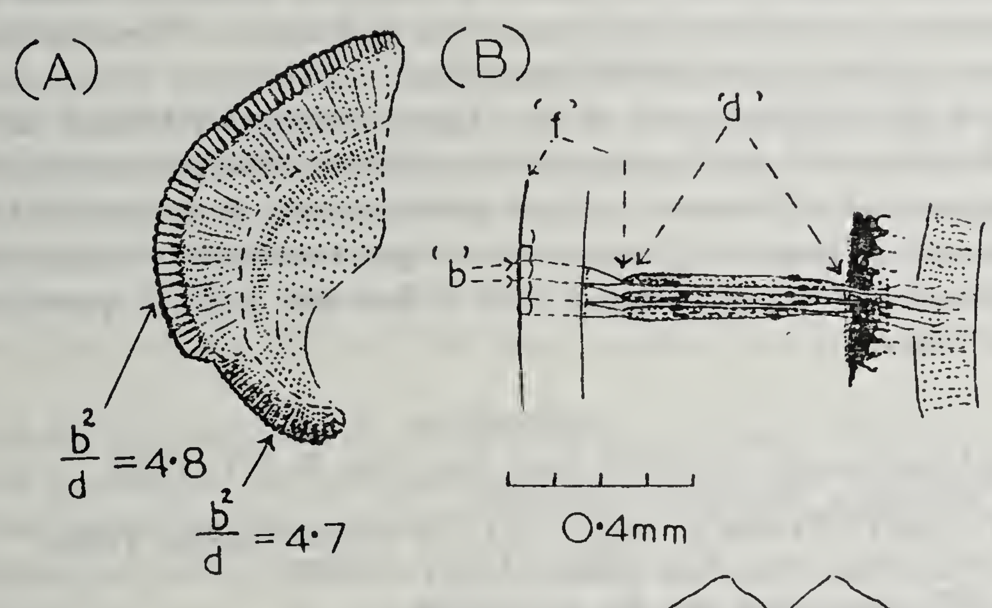

FIG. 1. (A) V.S. compound eye of *Bibio varipes* Meig. ♂.

(B) T.S. group of ommatidia in *Schistocerca gregaria* Fors. adult female, schematic but to scale.

(C) & (C′) ommatidial array in first instar and adult *Schistocerca*.

For "b", "f" and "d" see text.

Two situations were chosen in insect eyes where differences in ommatidial separation were as large as possible because the measurements involve considerable errors.

(1) *Different parts of the same eye showing large differences in ommatidial diameter. Simulium ornatum* Meig. (Diptera) male is an extreme example. Here "b" in the upper eye is 40 μ and in the lower eye is 16 μ while "d" is 255 and 42 μ respectively. $\frac{b^2}{d}$, for the upper eye is 6·3 and for the lower 6·1. *Bibio varipes* Meig. (Diptera) male gave values for the upper eye b = 26 μ, d = 143 μ; lower eye 16 μ, 54 μ. $\frac{b_2}{d}$ for the upper eye is 4·8 and for the lower eye 4·7.

(2) *Exopterygote eyes at different growth stages.* In *Carausius morosus* (Phasmida) adults were compared with larvae just hatched from the egg. For the first instar larva b = 24 μ, d = 47 μ, $\frac{b^2}{d} = 1{\cdot}25$, another insect gave $\frac{b^2}{d} = 1{\cdot}1$. For the adult b = 45 μ and d = 164 μ, $\frac{b^2}{d} = 1.23$, another example gave $\frac{b^2}{d} = 1{\cdot}11$. The intermediate instars are not so certainly recognised as in *Schistocerca gregaria* Fors. (Orthoptera) for which the following data were obtained.

Instar	1st	2nd	3rd	4th	5th	Adult ♀
b	18	22	25	30	34	38 μ
f	61	79	86	122	153	175 μ
d	96	147	166	246	319	473 μ
$\frac{b^2}{d}$	3·4	3·3	3·8	3·7	3·6	3·05

The last results are complicated by a change in the form of the array. In the first instar the array of facets is almost a square while in the adult it is perfectly hexagonal (Fig. 1, C,C').

One can say with certainty that the depth of the eye is relatively much greater in the eye of the same insect when the ommatidial separation is greater. There is a strong suggestion that the depth varies as the square of the separation.

The sections of the divided eyes of the Ephemeropteran *Chloeon dipterum* figured by Zimmer (6) and of the eyes of the Euphausiid Crustacean *Stylocheiron suhmi* Sars by Chun (2) both show a disproportionate increase in depth with increase in ommatidial separation. The present observations are all from the Neoptera but if one could add examples from Palaeoptera and especially Crustacea it would suggest that diffraction plays a part in compound eyes throughout the Arthropoda.

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BIOCHEMICAL AND TOXICOLOGICAL CHARACTERISTICS OF THREE PROTEIN COMPONENTS OF THE VENOM OF THE SPIDER *LATRODECTUS TREDECIMGUTTATUS**

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Latrodectus tredecimguttatus venom is known to be proteic in nature; the purpose of our study was to purify the toxic protein component(s) and to study their characteristics. The crude venom was a dialysed extract of poison glands in buffer: its toxicity was found to be approximately equal, on a body weight basis, to houseflies and guinea pigs, namely 10 to 12 LD50 doses/mg of protein/Kg of animals. Unless otherwise stated all operations were performed at temperatures as near as possible to 0°C. Column electrophoresis of the crude extract in borate buffer of pH 8·6 and elution with the same buffer resulted in the separation of five protein peaks. Peaks no. 1 and 4 were associated with toxicity towards houseflies, and the toxic principles they contained were called LV1 and LV2 respectively. LV1 caused in houseflies an immediate paralysis, which was reversible at low doses; LV2 caused a more retarded but irreversible paralysis. Peak no. 2 was associated with the toxicity towards guinea pigs. Its active principle was called LV3, and it caused in guinea pigs the characteristic symptoms of *Latrodectus* bite in mammals. The recovery with respect to the toxicity of the crude extract was around 100% for both the toxicity to houseflies and guinea pigs. Purification of LV1, LV2 and LV3 with respect to the crude extract was 4, 8 and 7·8 times respectively. To achieve a higher purification, a different method was adopted, combining gel filtration on Sephadex G-100 and ion-exchange chromatography on DEAE-Sephadex A-50. This allowed a much more complete separation of LV1, LV2, and LV3 than could be obtained by electrophoresis, as well as a higher purification (8, 8·5 and 23 times respectively, as compared with the crude extract). On the other hand the recovery was not so good ranging around the 50% of the original toxicities for both the housefly and the guinea pig. Possibly an inactivation had occurred, linked with the loss of the protecting action exerted by the accompanying proteins. The effect of different possible inactivating or protecting agents was tried on electrophoretically separated preparations of LV1, LV2, and LV3. Exposure for 21 hours at 26°C reduced the activity of LV1 to 1/10, and of LV2 to 1/2 of their original activity; LV3 was unaffected by this treatment.

The venoms of the spiders of the genus *Latrodectus* have been classified by various authors as "neurotoxic", on the basis of the symptoms they elicit, but their mechanism of action is still obscure. To gain some information upon the site of their action, the crude extract and electrophoretically separated preparations of LV1, LV2, and LV3 were tested on human epithelial cancer cells cultivated *in vitro*. The crude venom revealed itself highly toxic to the cells; lesions were histologically detectable after 24 hours incubation. The minimal active concentration was 0·25 μg of protein per ml in the culture medium; this effect was neutralised by a specific anti-serum. The same was true for LV1, and the minimal active concentration was 10 times lower. LV2 and LV3 were completely inactive towards the cells.

The finding of toxic principles causing neurological symptoms with such a high differential toxicity between mammals and insects may be useful for the study of the structural or functional differences between the nervous systems of these animals.

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LATRODECTUS (ARACHNIDA) VENOM IN INSECT IMMUNITY STUDIES

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Two groups of *Periplaneta americana*, respectively nymphs and adult males, were repeatedly injected with sublethal doses of *Latrodectus tredecimguttatus* crude venom. No significant increase in the cockroaches' LD_{50} value, nor any *in vitro* antitoxic property by the insects' blood was observed. The antitoxic action was assayed by injecting the treated cockroaches' blood incubated with the venom for 2 hours at 25°C at different dilutions into groups of houseflies. No immunisation could be observed either, in cockroaches vaccinated with one sublethal dose of venom and treated with a challenge dose at 24-28 hours.

The failure to obtain any *in vivo* immunity or any *in vitro* neutralising effect by blood of cockroaches injected with *Latrodectus* venom may be due either to a low antigenic property of the spider's venom toward *P. americana*, or to a lack of ability of producing an immunological response by the cockroach, or to inappropriate immunisation technique employed in the experiments, or by a combination of these causes.

Groups of houseflies were injected with a low dose of crude venom and reinjected at different time intervals with a challenge dose of *Latrodectus* venom. Mortality of 24 hours after the 2nd injection has been compared with that of flies treated with a 1st injection of saline followed by a challenge dose of venom. Vaccinated houseflies developed within 24 hours a low but significant degree of immunity against the venom. This immunity appeared to increase between 24 and 48 hours and to last 96-120 hours. It is difficult to say whether this resistance builds up during the first hours following the 1st injection since there is, up to 7 hours, an accumulation of effect of the venom, which phenomenon may mask the immunity process. The trend of the protective immunity values plotted against time is compared with similar curves, reported by other authors, on the immunity of *Oncopeltus fasciatus* and *Galleria mellonella* against bacteria (*Pseudomonas aeruginosa*).

Latrodectus venom thus represents the second animal toxin which has been shown to induce a protective immunological reaction in insects. *Musca domestica* is the first species of the order Diptera showing protective immunity following vaccination.

SECTION 4.—GENETICS AND CYTOLOGY

The following paper was read but the authors did not wish for publication in these Proceedings; it will be incorporated in a forthcoming monograph of the Cimicidae:

Usinger, R. L., and Ueshima, N. (U.S.A.). Cytotaxonomy and the species concept in Cimicidae.

BIOCHEMICAL AND PHYSIOLOGICAL GENETICS

CONTROLE CHEZ LES INSECTES DES HORMONES DE CROISSANCE PAR LES PTERINES AGISSANT PAR INDUCTION OU PAR REPRESSION EN FONCTION DE LA TEMPERATURE ET DE LA PHOTOPERIODE

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L'association ptérines/hormones de croissance contrôle de manière impérative la division cellulaire. Les variations de ce rapport en fonction des facteurs extérieurs modifient l'équilibre cellulaire dans un sens ou dans l'autre. Les perturbations apportées à ce rapport, spontanées ou artificielles entraînent la carcinogenèse.

C'est ainsi que l'injection d'acide folique pendant l'hibernation chez des chrysalides en diapause provoque la formation de tumeurs mélaniques. De ces tumeurs on peut extraiter un facteur ultrafiltrable, ultracentrifugeable et retransmissible à d'autres chrysalides. Ce facteur induit n'est pas spécifique, on peut le greffer chez la Drosophile, il se transmet alors héréditairement. Le sex ratio est modifié en même temps qu'il y a apparition de tumeurs léthales toujours chez les larves mâles (mélanoma des testicules ou du tube digestif, accompagnés de leucémie). Le sex ratio est caractérisé par la diminution des mâles. L'examen de la répartition de ce rapport dans la descendance montre qu'elle ne suit pas la loi de Mendel, mais est parfaitement anarchique et constante de génération en génération. Ce phénomène se manifeste même après une série de backcrosses successifs sans atténuation. On croise la souche tumorale avec des éléments sains qui n'ont jamais été traités:

Les générations F_2 données par le croisement *a* montrent un phénomène stabilisé toujours identique à lui-même, alors que les générations F_2 du croisement *b* montrent une disparition progressive du phénomène; c'est donc bien un processus d'hérédité cytoplasmique qui est suscité. Le facteur anormal induit par les ptérines dans ces conditions est détruit par la désoxyribonucléase, il n'est pas sensible à la ribonucléase, ni aux enzymes protéolytiques. Les broyats de tumeurs obtenus à partir d'extraits par le phénol, par la technique de Gierer et Schramm gardent leur activité; il se formerait donc des séquences d'ADN portées par des particules anormales. Ces particules sont légères, il faut en effet les centrifuguer à 26,000 g entres 2 et 4 heures pour le faire tomber au fond et la taille des particules se situerait donc entre 35 et 45 mμ. La sédiment par gradient de densité confirme que les particules sont de petite taille, car elles se concentrent dans deux zones bien définies, l'une à 1,4 cm. du ménisque en haut de la deuxième phase de sucrose, la 2e à 5 cm. du ménisque à la limite inférieure de la 3e phase du sucrose.

Il semble que l'ADN induit par les ptérines en l'absence d'hormones de croissance régulatrices transmet des informations anormales aux ribosomes car il y a des modifications de l'activité enzymatique des tissus: la tyrosinase ne se localise plus dans les tissus normaux, on constate en effet que les tumeurs sont entourées d'une enveloppe de tissus mélanisés et sclérifiés très durs. Les tissus touchés sont les dérivées de l'ectoderme (stomodeum et proctodeum, enveloppe folliculaire du testicule).

En même temps le métabolisme des ptérines est perturbé. Une étude des pupes montre la disparition d'une ptérine bleu-vert voisine de la xanthoptérine et augmentation de la bioptérine et de ses dérivés.

Le dosage de la xanthoptérine-oxydase montre une forte diminution de l'activité de celle ci dans la souche porteuse de tumeurs. (Technique Glasman et Mitchell).

Les premières indications données par l'étude du métabolisme suggèrent que les ribosomes reçoivent une information modifiée et modèlent alors les protéines d'une manière différente, au moins dans certains organes, ce qui pourrait expliquer les réponses différentes des tissus.

Chez *Pieris* en état de diapause, le déséquilibre provoqué par l'absence d'hormones de croissance et l'apport de co-facteurs ptériniques réprimant ou activant certains des processus de synthèse (par un mécanisme encore inconnu) se traduit par l'apparition d'ADN anormal qui donne une information déviée aux ribosomes et entraîne des changements dans l'activité enzymatique. L'étude faite chez la Drosophile prouve que les séquences d'ADN nouvelles induites sont stables, douées d'une "virulence" telle qu'elles sont capables de transformer à leur tour l'équilibre cellulaire de cette espèce chez qui elle est greffée et qui a pourtant son rapport hormonal normal (puisque dans le cas des Drosophiles il n'est pas question de déficience due à une diapause).

TRITIATED THYMIDINE STUDIES ON INSECT HEMOCYTES

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The large milkweed bug, *Oncopeltus fasciatus*, was the experimental animal in these studies. Tritiated thymidine was injected into different groups of bugs on the day of molt into the fifth instar and on successive days after the molt for the duration of the stadium. Two experimental and two control insects from each group were sacrificed and hemolymph smears were made every 24 hours after the injection for the duration of the stadium. The slides were dipped in Kodak NTB2, stored in light tight boxes at 4-8°C for eight days, developed in D19, rinsed in acid fixer and water, and stained with Giemsa blood stain for 15 minutes.

The slides were examined and 150 cells on each slide were counted. The percentage oj hemocytes with tritiated thymidine incorporation, the percentage of mitotic figures, and the percentage of mitotic figures with tritiated thymidine incorporation were determined. A hemocyte was considered to have radioactive incorporation if the number of reduced silver particles in the emulsion over the nucleus was at least twice the background.

With one exception there was no appreciable incorporation until 48 hours after the injection of tritiated thymidine regardless of when the injection was given. This delay in incorporation was surprising in view of the fact that most investigators report that the thymidine is used within 60 minutes of injection. There is the possibility that the majority of the hemocytes are formed in a hemopoietic organ or site and then released into the circulating hemolymph.

In most cases the peaks of hemocytes with incorporation occurred on the 5-6 days and the 9-10 days after the molt into the fifth instar regardless of when the injections were given. When the tritiated thymidine was injected on the ninth or tenth days of the stadium, i.e. 48 or 24 hours before the adult molt, there was no incorporation although there was incorporation on these days when the injections were made earlier in the stadium. The lack of incorporation at these times substantiates our previous statement of a delay of at least 48 hours after injection before incorporation appears in the hemocytes.

When the tritiated thymidine was injected on the fourth or fifth days of the stadium, which lasted 10-11 days under our laboratory conditions, there was very little incorporation for the entire stadium. This suggests that there is little DNA synthesis in the hemocytes or hemopoietic tissue at this time or that another tissue is much more active mitotically at this time and it is utilising the tritiated thymidine.

When the injections were made early in the stadium there was a second peak of incorporation around the ninth or tenth day after the molt and approximately four or five days after the first peak of cells with incorporation.

There was a consistent low level of mitosis throughout the stadium. The percentage of mitosis, or mitotic index, varied from 0 to 15. We could see no correlation of the higher peaks of mitotic activity with age, time of injection, time of day when the hemolymph was taken, or high peaks of thymidine incorporation. The percentage of mitosis with tritiated thymidine incorporation varied from 0 to 100.

GENETIC CONTROL OF AMYLASE ACTIVITY IN *DROSOPHILA MELANOGASTER*

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Amylase activity in *D. melanogaster* is controlled by a single locus, *Amy*, on Chromosome II (1, 2 and 4). Several alleles differing in activity have been described and changes during development indicated. Alleles are characterised by different banding patterns in agar gel electrophoresis (3 and 5). Thus, *Amy* alleles offer several advantages for studying genetic control of enzyme production in a higher organism: ease of enzyme assay, a variety of alleles

with quantitative and qualitative differences, and the possibility of relating "puffing" patterns of polytene chromosomes with enzyme activity.

I analysed *Amy* alleles derived from the following strains: Oregon-R, Swedish-B, Canton-S, Seveten, *adp*^{60}, *Cy*/*adp*^{fs}, *cn bw*, *Amy*^{S} (Hikone), *Amy*$^{+}$ (Hikone), and *Amy*^{wh}. The last three were received from Prof. Kikkawa. Chromosomes I and III were made coisogenic in all lines. Tests made on flies raised axenically verified that the amylase activity could not be attributed to micro-organisms associated with the flies.

Linkage data was obtained from the following cross: $+^{cn}$ *Amy*^{S}$+^{adp}$ × *cn Amy*^{cb} *adp*^{60} (*Amy*^{S} has strong activity while *Amy*^{cb} has weak; heterozygotes do not overlap with *Amy*^{cb} homozygotes in activity.) F_1 females were test-crossed to *cn Amy*^{cb} *adp*^{60} males and their progeny (N = 524) individually tested for amylase. Results indicate *Amy* lies 6·1 c.o.-units to the left of *adp* (located at 2-83·4), placing it at 2-77·3. The location as previously reported was based on either indirect analyses or the use of a formula that omitted double c.o.-types.

Starch-iodine colorimetry was used for quantitative analysis of *Amy* strains with two significant modifications of Kikkawa's methods. Flies were homogenised in phosphate buffer, pH 6·8, saturated with p-chloromercuribenzoic acid (PCMB) to inhibit glycogen phosphorylase activity that might be interpreted as amylase. Iodine tests made on supernate ± PCMB indicated that although most activity (mg. starch decomposed/25 min. at 25°C./mg. tissue) could be attributed to amylases, a small fraction was lost when the phosphorylase inhibitor was present. More significant was the enhancement of activity found on the addition of Cl ions to the reaction mixture. Under these conditions, activities among the alleles ranged from a low 0·045 mg. starch/25 min. mg. tissue for *Amy*^{OR} to a high of 0·677 for *Amy*^{S}. Hybrids between two alleles had activities roughly intermediate between them.

Relative amylase activity in tissues and organs of larvae and adults was determined for the *Amy*^{S} strain. In both stages, most activity was found in blood and midgut. For adult females, activities in decreasing order were: blood, ventriculus, salivary glands, thoracic muscles + fat body + body wall, head + esophagus, abdominal fat body + body wall, Malpighian tubules, ovaries, rectum, and anterior intestine (none in crop or reproductive tracts and glands). In larvae, the order was: blood, midgut, fat body, salivary glands, Malpighian tubules, and remainder (0·07% of total).

Changes in activity throughout development were determined for the *Amy*^{S} strain. Activity in newly laid eggs was 0·001 mg. starch/25 min./egg, rising to 0·003 by the end of embryonic development. Activity gradually increased during instars I and II of larval life and showed a marked increase by the late third instar, reaching values as high as 0·704 mg. starch/25 min./larva. A rapid drop followed puparium formation, "prepupal" activity being 0·130 and pupal activity falling off to 0·053 prior to adult emergence. After emergence, activity continued to rise until the second to third day.

Banding patterns formed by *Amy* alleles were analysed by use of acrylamide gel disc electrophoresis. The method of Ornstein and Davis (6) was employed but modified to include 0·2% soluble starch in the small pore gel. After electrophoresis, gels were removed from tubes, incubated for varying time intervals at 37°C, and stained with iodine. Unstained bands appeared where amylase activity was present. As in the agar gel studies of Kikkawa and Ogita, a total of seven bands were associated with amylase activity. The number and relative activity of these isozymes differed between alleles. More of them appeared in the *Amy*^{S}, *Amy*$^{+}$, *Amy*^{wh}, and *Amy*^{ad} strains than were described by Kikkawa and Ogita (pers. communic.) so that homologies remain obscure. Hybrids, for the most part, showed additive banding patterns although some possible exceptions will be discussed.

Population cage studies of strong and weak *Amy* alleles linked with *adp* alleles indicate that they not only can persist in a balanced polymorphic state but also give evidence of an interaction between the *Amy* and *adp* loci.

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GENETIC STUDIES OF OOGENESIS IN *DROSOPHILA*

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Lozenge (*lz*) is a sex-linked, recessive mutation located at 27·7. The primary effect of this gene is upon the eye morphology causing modification of the facets which results in a deepened coloration and rather "rough" appearance. Numerous secondary or pleiotropic effects are associated with the mutant and they include such seemingly unrelated features as a reduction or loss of the tarsal claws and pulvilli; absence or modification of the spermathecae and accessory glands; and generally a marked reduction of the female reproductive capacity. Oliver (1940) demonstrated that two of the *lozenge* alleles could recombine with each other and thus the *lozenge* mutants represented a complex or pseudoallelic series. Green and Green (1949 and '56) established that each of 18 independent mutants could be assigned to one of three recombinationally discrete loci. However, two alleles, lz^{49h} and lz^{50e}, failed to fulfill the accepted criteria of allelism in that these two exceptions produced near wild-type phenotypes when compounded with any of the other *lozenge* alleles. These two mutants were further distinctive in that they possessed both spermathecae and normal tarsal claws. The finding of an autosomal suppressor gene which markedly increased the reproductive potential of a sterile *lozenge* mutant without restituting the accessory reproductive structures, led to the demonstration of primary ovarian abnormalities in the lz^{34k} mutant (Bender and Green 1960 and 1962). Justification for considering a phenogenetic study which would entail considerations of the female reproductive physiology of the various *lz* alleles thus seemed very strong.

This present study involved the utilisation of twelve *lz* mutants which represented all of the known *lz* sub-loci. These were crossed in all possible permutations. The resulting 60 heterozygous classes and 12 homozygous classes were then studied as to the effect upon reproductive capacities, internal reproductive morphology and oogenesis. These data were then collated with those for eye morphology and tarsal claw effects. Pathologies of the ovarian tissue were found in all sterile alleles and compounds. The major differences primarily being the degree to which the tissues were effected and the age of onset. Abnormal ovarian cysts were found which suggested the linking of the imaginal corpus allatum with the primary cause of *lz* ovarian abnormalities. Implantation of normal corpus allata into *lz* hosts was found to have a strong sparing effect. During the course of these studies a genetic factor was found associated with the lz^{34k} mutant which when compounded with the lz^{50e} allele results in a typical *lozenge* phenotype rather than the exceptional near-normal phenotype. Studies of the reproductive physiology of this compound suggest the possibility of a rearrangement or further inactivation involving both the *amx* and lz^{50e} loci as being responsible for this interaction.

GENETICS OF INSECTICIDE RESISTANCE

RESISTANCE TO CHLORINATED INSECTICIDES IN ANOPHELINE MOSQUITOES

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Specific physiological resistance to chlorinated hydrocarbon insecticides has been recorded in some of the areas of distribution of 37 species of anopheline mosquitoes, 19 of which are vectors, or suspected vectors of malaria. Two types of resistance are involved, dependent on at least two separate genetic factors. One confers a moderate degree of resistance to DDT and its analogues. The other usually confers a high degree of resistance to dieldrin and related cyclodiene compounds and a moderate degree of cross-resistance to gamma-BHC. Both types of resistance can occur in the same individual mosquito and a feature of recent analyses of cases of resistance is an increase in the frequency of this double-resistance. Of the 19 vector species referred to, 2 have shown resistance to DDT only, 6 to dieldrin only, and 11 to both groups of chlorinated hydrocarbons.

The mode of inheritance of dieldrin-resistance has been studied in detail, using laboratory colonies, in six anopheline species: *Anopheles gambiae*, *A. albimanus*, *A. quadrimaculatus*, *A. stephensi*, *A. sundaicus*, and *A. pharoensis*. A single autosomal genetic factor showing incomplete dominance has been demonstrated in all six species, using two discriminating dosages of the insecticide for phenotype recognition, the lower one killing susceptibles but not heterozygotes, the higher killing the latter but not homozygous resistant individuals. Monofactoriality has been confirmed by repeated backcrossing to the susceptible parent and exposing the offspring to the lower discriminating dosage. No rise in mortality in successive generations of this process occurs.

Dominant dieldrin-resistance, again dependent on a single genetic factor, has been found in *A. gambiae* from some areas of West Africa. Usually it is of a high degree (1). Whether the genetic factors responsible for the different types of dieldrin-resistance in *A. gambiae* are allelic or not remains to be established.

DDT-resistance has been studied in 5 of the 6 species listed (there is as yet no resistance to DDT in *A. gambiae*). Again a single, autosomal, genetic factor is involved but this is more variable in its genetic expression. The commonest type so far encountered is the recessive one but partial dominance can be seen in *A. pharoensis* from Egypt. More complete dominance is shown by *A. stephensi* from Iran.

Resistance in one and the same population to both DDT and dieldrin has been studied in *A. albimanus*, *A. quadrimaculatus*, *A. stephensi* and *A. pharoensis*. Double-resistant *A. albimanus* and *A. quadrimaculatus*, when crossed with their susceptible strains show the different inheritance mechanisms involved in the two resistances: dieldrin-resistance shows partial dominance, DDT-resistance its recessive character. This in itself demonstrates the separate identity of the two genetic factors, but proof has been given by the actual isolation from a population of *A. albimanus* showing the two resistances, of one colony showing DDT-resistance and dieldrin-susceptibility and another showing dieldrin-resistance and DDT-susceptibility.

It seems almost certain that the genetic factors for DDT and dieldrin-resistance are on the same chromosome and are probably closely linked. This may mean in practice that selection with one insecticide may increase the frequency of individuals resistant to the other. An attempt to show such a linkage, in the absence of suitable marker genes, has been made by crossing DDT-resistant and dieldrin-resistant strains of *A. quadrimaculatus*. The hybrid obtained was backcrossed to the DDT-resistant parent and the offspring exposed to the lower discriminating dosage of dieldrin and to the discriminating dosage of DDT. Those mosquitoes surviving each of these dosages were then exposed to the opposite insecticide. Independent assortment would be indicated by equal kills on successive exposures to DDT and dieldrin. Complete linkage would be indicated by a complete kill on the second exposure. In fact an incomplete kill, but higher than the first, resulted from the second exposure.

The genetic nature of physiological resistance implies that the speed of selection of resist-

ance will depend on the original frequency of the resistance gene, the expression of the gene (dominant or recessive), the degree of resistance imparted by it, particularly in the heterozygous state, the efficiency of the insecticide and the behaviour of the insect. Thus a highly efficient insecticide like dieldrin, applied against a population containing dieldrin-resistant individuals, will rapidly select out a resistant population from quite low, original frequencies (and the existing evidence points to dieldrin-resistance being far from rare in untreated populations (2)). In contrast, a less efficient insecticide like DDT (because of its irritant nature) applied against a population containing DDT-resistant individuals, whose degree of resistance even in the homozygous state is not very high and in which the heterozygote may be almost as susceptible as the susceptible individual, will take much longer to select out a resistant population. This is in fact what has occurred in the field and accounts for the rapid appearance and greater incidence of dieldrin-resistance.

It seems, therefore, that of the insecticides available at the present time, DDT must be the insecticide of first choice in malaria eradication campaigns. Then, even if DDT-resistance is present in the population, its selection may be so slow that eradication of the malaria parasite may be achieved before the proportion of resistant individuals is sufficient to continue its transmission. There is even some evidence that DDT will continue to inflict sufficient mortality among the DDT-resistant individuals of an inefficient vector species to intercept malaria transmission by such individuals.

With a highly efficient vector species like *A. gambiae*, on the other hand, there is evidence that DDT, even in the absence of resistance, does not inflict a high enough mortality to interrupt malaria transmission. This evidence, coupled with the presence already of dieldrin-resistance in this species over a wide area of West Africa makes the future prospect of eradication in this part of Africa most uncertain, unless new insecticides are forthcoming. Strangely enough, dieldrin-resistance has not yet been recorded in *A. gambiae* in East Africa in spite of a high selection pressure in some areas. Thus dieldrin or BHC might still be used with success over a considerable area of Africa, though there is always the risk of spread or importation of dieldrin-resistance from the West.

In conclusion it might be said that in regions in which malaria eradication programmes are already being carried out (and there are no such programmes as yet in Africa) insecticide resistance is limited to comparatively small areas and has not yet presented an insuperable obstacle.

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GENETICAL STUDIES ON INSECTICIDE RESISTANCE IN MOSQUITOES

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Numerous genetical studies on mosquitoes have indicated that resistance to insecticides is monofactorial in its inheritance. These experiments have taken the form of mass matings between resistant and susceptible strains. It seemed interesting therefore to look for confirmation of the monofactorial mechanism in the results of single pair matings. The DDT-resistant Trinidad strain of *Aedes aegypti* was chosen for study and preliminary experiments took two directions.

(1) Single pair sib-matings within the Trinidad strain.

(2) Single pair matings between the Trinidad strain and the QS susceptible strain.

Mass crosses had indicated that the mode of inheritance for DDT resistance in the Trinidad strain was a semi-dominant gene. On this basis it was possible to calculate the expected form of the F_2 concentration/mortality regression lines from the single pair matings, and to observe whether the actual results corresponded with those expected.

(1) The first series of matings indicated that the Trinidad strain was very heterogeneous. Fully susceptible F_2 progenies were obtained, also F_2 progenies of high resistance (L.C. 70 > 80 p.p.m.) and F_2 progenies of intermediate resistance. If a single gene was operating, the Trinidad strain was clearly heterozygous. In fact the variation was too great to be attributed

to a single gene segregating normally. Many F_2 lines showed well marked inflexions suggesting genetic segregation but in only a small minority of matings did the form of the F_2 regression line approximate to that expected from segregation at a single locus.

(2) Confirmation of these findings came from the results of single pair crosses between the Trinidad and QS strains. Moreover quite apart from individual variations between F_2 progenies, an overall difference was observed between the reciprocal crosses. All the F_1 and F_2 progenies derived from Trinidad females were more resistant than those derived from Trinidad males.

From these two series of experiments it was concluded that DDT resistance was not due to a single gene segregating normally, although the distinctness of the inflexions on the F_2 regression lines suggested that the number of genes involved was probably small.

Special attention was paid to one F_2 (F_2165), which (atypically) had segregated very clearly into three phenotypes, suggesting a parental cross R/+ × +/+. F_2165 was selected at 5 p.p.m. and the resulting $F_3(169)$ was used in a series of crosses and backcrosses which established its homozygosity (or near homozygosity) for resistance. The L.C.50 of F_3169 was 0·5 p.p.m.

Subsequently it was established that the dominance of F_3169 resistance was modified by a factor located at (or near) the *y* locus on chromosome2, resistance being recessive in yellow (y/y) larvae and semi-dominant in the heterozygous wild type (+/y) larvae.

+/y R/R × y/y +/+
↓
+/y R/+ + y/y R/+
(resistance semi-dominant) (resistance recessive)

Conclusions

(1) That the use of single pair matings reveals genetic variation which is not evident from mass matings.

(2) That some reservation should be placed on the use of the mutant *y* in linkage studies with resistance alleles.

BIOCHEMICAL GENETICS OF INSECTICIDE RESISTANCE IN CULICINES

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Insecticide resistance has been developed by 15 species of culicine mosquitoes, 13 of them to DDT, 13 to the BHC-cyclodiene group, and 4 to organophosphorus compounds. Our studies on the biochemistry and genetics involved have been performed by Z. H. Abedi, J. R. Duffy, P. G. Fast, N. H. Khan, M. A. Q. Khan, T. Kimura, W. Klassen, F. Matsumura, M. K. K. Pillai and T. Tadano.

DDT-resistance in *Aedes aegypti* is inherited as if due to a single principal gene allele; the hybrids are intermediate in all strains studied, but there is considerable overlapping between genotypes. Backcrosses involving strains marked with visible mutants showed the principal gene for DDT-resistance to be linked not with *black-tarsus* on chromosome III, nor with sex on chromosome I, but with *yellow* and *spot* on chromosome II at crossover distances of 20 to 25 units.

The principal mechanism of DDT-resistance in *A. aegypti* is detoxication to DDE. The resistance level of various strains was proportional to their dehydrochlorinating activity both *in vivo* and *in vitro*. The DDT-dehydrochlorinase enzyme in this culicine resembled that in the housefly in its optimum pH, in working better on DDD, and in being inhibited by DMC and WARF-Antiresistant. But it required more glutathione protection than the housefly enzyme, and differed from it in dehydrochlorinating ortho-chloro-DDT but not deutero-DDT. The only DDT metabolite *in vitro* and *in vivo* is DDE, although some Kelthane appears in very resistant strains.

Supplementary resistance mechanisms include an increased larval excretion of peritrophic membrane in Caribbean strains, a slightly increased phospholipid content in a Malayan strain, and decreased absorption in a DDT-resistant strain developed by malathion selection.

The Malayan strain is normally somewhat DDT-tolerant, producing considerable DDE; its DDT-resistant substrains produce little more DDE. However its DDT-resistance showed the usual chromosome-II linkage relationships, and when crossed with Caribbean strains there was no increase in resistance in the F_1 and F_2, nor in heterogeneity in the F_2.

WARF-Antiresistant is initially a DDT syncrgist against DDT-resistant strains, but eventually they become resistant to the mixture. Crosses of the Mixture-resistant with the DDT-resistant strains do show increased resistance in the F_1 and F_2, although their principal gene still manifests the same chromosome-II linkage relationships. Evidently Mixture-resistance is characterised by a different set of modifier genes; indeed factorial analysis showed chromosome III to be no less important than chromosome II. These different modifiers must take some time to accumulate, since the first 2-3 generations of mixture selection temporarily reverses the DDT-resistance. The importance of modifiers in strict DDT-resistance was revealed in the Malayan strain, where the high DDT-resistance initially produced by the first selections showed a readiness to revert on relaxation of pressure. The first DDT plus-variants to be produced by the selection were handicapped by a low oviposition and a low hatch; eventually this was corrected by the third cycle of selection and relaxation, when the plus-variants regained a normal biotic potential, and thus the resistance was stabilised.

In other culicines, DDT-resistant *A. taeniorhynchus* produced more DDE than susceptible larvae, and resistant *A. nigromaculis* showed increased DDT-detoxication. DDT-resistant larvae of *Culex tarsalis* and *C. fatigans* produce DDE as the only metabolite, and the amount produced *in vitro* is proportional to the resistance level. *In vivo* this difference is shown in *tarsalis*, but in *fatigans* the original strains are already active in producing DDE. As in *A. aegypti*, DDT-resistant *C. fatigans* cannot withstand deutero-DDT. The DDT-resistance in *C. tarsalis* has been traced to a single recessive factor; while in *C. fatigans* it is associated with a single dominant factor.

Dieldrin-resistance in *Aedes aegypti* is inherited monofactorially, the hybrids being exactly intermediate. The gene is located on chromosome II, 15 crossover units from *Gold*, 19 from *yellow* and 22 from *spot*. Initially dieldrin-resistance could not be separated from the DDT-resistance already associated with it in the Puerto Rico strain, whether by selection with dieldrin or with DDT coupled with backcrossing to a susceptible strain. Eventually however a Dld-R DDT-S strain and a Dld-S DDT-R strain were obtained; and crosses between these two, and between the doubly resistant and the doubly susceptible strains, showed that the resistances were about 4 crossover units apart, and the distance *DDT* to *yellow* was 23 units compared with 19 units for *Dieldrin* to *yellow*. Dieldrin-resistance in this strain was accompanied by a higher content of neutral fat in the larvae.

Increased tolerance to the OP compounds malathion and parathion induced in *A. aegypti* by laboratory selection has been found to be associated not with increased detoxication but with decreased absorption in Caribbean, Malayan and a West African strain. The cross-resistance to DDT simultaneously induced was found to be associated with decreased DDT absorption as well as increased DDT-dehydrochlorinase content. The inheritance of the malathion-tolerance character, for which the hybrids are intermediate, indicates that polygenes are involved, with the main influence from chromosome II and an influence from chromosome III which is significant in females. Estimates of linkage show crossover values of about 35 from *yellow* and 33 from *Dieldrin*, and thus they do no more than confirm the influence of chromosome II.

The specific malathion-resistance of *Culex tarsalis* proved to be due to a single factor, almost completely dominant; its resistance mechanism was a greatly increased carboxyesterase activity in detoxifying malathion, the only OP insecticide open to this type of hydrolysis. The mutant carboxyesterase of resistant *C. tarsalis* was purified by DEAE cellulose column chromatography and compared with the normal carboxyesterase. Produced in 13-fold molar quantity, it proved to have the same molecular weight of 16,000, and not to differ in polypeptide "finger-prints", U-V absorption or electrophoretic characteristics. However, it was more heat-labile than the normal enzyme, and was precipitable at pH 5 which the normal is not; these differences are entirely analogous to those discovered in the mutant tryptophane-synthetase of *Escherichia coli*. Thus the effect of the allelism in *C. tarsalis* is to produce more of a "softer" enzymic protein.

INSECTICIDE RESISTANCE FACTORS AND GENETIC LINKAGE IN *BLATTELLA GERMANICA* (Dictyoptera)

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Blattella germanica (L.), is a species known to be resistant to both groups of chlorinated hydrocarbons, malathion, diazinon, entex, sevin, pyrethrum, and probably other insecticides in various laboratory and field populations. Previous studies have shown that some of these strains possess specific high level resistance to one or more insecticides.

The inheritance of resistance to aldrin has been examined in two strains of distinctly different geographical origin. In one strain (Texas) the parental resistance was approximately 500-fold that of the susceptible strain. The F_1 progeny from reciprocal crosses were intermediate between the parental lines and showed approximately 45-fold resistance at LC_{50}. No indication of sex linkage occurred. The F_2 and backcrosses were tested with a discriminating concentration of aldrin which killed only the susceptible genotype. In the F_2, 25% of the population was killed, while in the backcrosses either 50% or 0% mortality occurred, depending upon the parental stock involved. The data indicate that aldrin resistance is inherited primarily as a simple Mendelian autosomal semi-dominant trait.

Data obtained in the strain from Germany (Landstuhl) corresponded very closely to that for the Texas strain, although the former had only about 300-fold resistance, and the F_1 roaches were correspondingly slightly less resistant. A logical interpretation of the data is that this resistance is also inherited primarily as a simple Mendelian autosomal semi-dominant trait. Tests for allelism indicate that these two aldrin resistances are allelic.

DDT resistance in the Landstuhl strain has previously been shown to be inherited as a simple Mendelian autosomal recessive with the hybrids being slightly more resistant than the susceptible parent. Modifiers are probably involved.

Four morphological markers have been identified and analysed genetically. It has been shown that balloon-wing, orange-body and red-eye are all inherited as simple autosomal recessives. Pro-wing is a semi-dominant lethal. Balloon-wing, orange-body, and pro-wing are located on different chromosomes. Red-eye is independent of balloon-wing and orange-body. Red-eye and pro-wing have not been analysed for linkage.

Aldrin resistance is independent of red-eye, orange-body, and pro-wing. Preliminary indications are that it is not closely linked with balloon-wing, but independence has not yet been demonstrated. DDT resistance is independent of orange body, but is linked with balloon wing at a distance of 30-40 map units. DDT resistance and aldrin resistance do not appear to be linked.

From this information one linkage group has been identified involving DDT resistance and balloon-wing. Several other linkage groups are also indicated by the independence of many of the traits mentioned above. It is apparent, however, that more traits are needed to definitely establish these linkage groups.

SOME CASES OF RESISTANCE CAUSED BY THE ALTERATION OF ENZYMES

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Three cases of genetic alteration of an enzyme causing resistance have been studied in our laboratory. Two of these deal with organophosphorus (OP) resistance, the third with the genetics of DDT-dehydrochlorinases (DDT-ases). Since the studies on OP-resistance have been published elsewhere, they will be mentioned only briefly whereas the recent results on DDT-ases will be described in greater detail.

I.—*OP-resistance in Tetranychus urticae Koch.* Smissaert (1) found that in some strains of the two spotted spider mite the monogenetic OP-resistance is caused by the production of a cholinesterase which reacts much more slowly with OP inhibitors than does the S cholinesterase.

II.—*OP-resistance in Musca domestica L.* In the housefly several types of OP-resistance are mainly caused by different alleles of a gene on chromosome 5 that controls the presence of ali-esterase A. The mutant alleles, instead of producing the esterase, form degrading enzymes attacking different OP-compounds. There are also alleles producing degrading enzymes differing in efficiency (2, 3, 4).

III.—*DDT-resistance in Musca domestica.* In the housefly most DDT-R strains contain DDT-ase (5). A study was undertaken on the possible existence of allelic DDT-ases in different strains. The extreme sensitivity of the gas-chromatographical estimation method for DDT and DDE enables the detection of DDT-ase activities as low as one thousandth of that of a single R-fly. Acetone powders were incubated under the usual conditions with colloidal suspensions of DDT or other substrates. After the incubation period extracts were made and injected into the chromatograph for estimation of substrate and dehydrochlorination product.

DDT-ase levels were determined in three strains: L (DDT-synergist R strain from Kearns); Fc (DDT-synergist R strain (3)) and ro;acv;cm (Japanese S strain with markers on chromosome 2, 4 and 5). The data obtained with acetone powders of these strains are summarised in table 1.

TABLE 1.

Activity and inhibition of DDT-ases of 3 strains of housefly

Activity (moles $\times 10^8$ per fly per hour)		strain	
Substrate	L	Fc	ro;acv;cm
DDT	51	2·5	0·17
TDE*	217	0·5	0·07
Br-TDE*	355	144	5·9
Inhibition (%)			
Concentration (M) $\times 10^6$**	L	Fc	ro;acv;cm
*DDT - DMC**			
50–50	99·4	37	—
50– 5	95	3	—
Br-TDE - DMC			
50–50	97	30	22
50– 5	92	−16	−10

*TDE = 1,1 dichloro-2,2-bis-(p-chlorophenyl)-ethane
Br-TDE = 1,1 dibromo-2,2-bis-(p-chlorophenyl)-ethane
DMC = bis-(p-chlorophenyl)-methylcarbinol
**DDT and Br-TDE as a colloidal suspension, DMC in solution.

Widely different DDT-ase levels are found in the three strains. The production of the DDT-ases in strains L and Fc is controlled by allelic or closely linked genes on chromosome 5, called D-ase^{L} and D-ase^{Fc}. From the table it appears that these DDT-ases differ in substrate specificity and susceptibility to inhibitors, whereas no important differences show up between Fc and ro;acv;cm. Therefore there must be a qualitative difference between the enzymes in L and Fc, but Fc and ro;acv;cm could differ only quantitatively. Whether the enzyme in ro;acv;cm is produced under the control of another allele of the D-ase gene is not known, but it resembles the other DDT-ases in that it also requires glutathion whereas it is not activated by cysteine. Probably the DDT-ases of strains Fc and ro;acv;cm can be regarded as wild-type enzymes, from which the more active DDT-ases like that of strain L originated by mutation. The study of these enzymes with low activity is greatly facilitated by the use of Br-TDE as a substrate, which is degraded by these enzymes about 40 times faster than DDT. It was found that the resistance of strain L is largely determined by chromosome 5, probably by the D-ase^{L} allele. The resistance in strain Fc is not controlled by factors on the 2nd, 4th or 5th chromosome, and the low DDT-ase activity probably contributes little to it.

The existence of a series of enzymes with different breakdown activities in OP and DDT resistant flies poses the problem whether the breakdown enzymes with the high activities could have arisen by more than one mutational step within the same cistron. This could be so if the intermediate levels of activity had sufficient survival value to enable their spread upon

selection. It might be surmised that in this way so called single-gene resistance could develop gradually by a number of consecutive steps.

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INVESTIGATION OF THE RESISTANCE PATTERN OF A FLUOROACETATE-RESISTANT HOUSE FLY STRAIN

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An insecticide susceptible strain of the house fly (*Musca domestica* L.) was selected for fluoroacetate resistance. Resistance patterns to various insecticides, obtained after selection with fluoroacetate for 25 generations have been reported (1). It is the purpose of this communication to discuss results of selection for an additional 40 generations.

After 25 generations of exposure to fluoroacetate, resistance to DDT increased 75 fold. This high level was maintained for two years or another 32 generations of exposure, independent of whether selection for fluoracetate was continued or whether the flies were reared without any further selection. For methoxychlor the picture is similar except that the highest level of resistance obtained was only about 20 fold, declining gradually to about 10 fold at the end of these series of experiments.

With dieldrin quite a different picture is evident. An 8,000 fold increase was obtained after 25 generations of selection with fluoroacetate.

However, when selection with fluoroacetate was continued, resistance to dieldrin fell very sharply. On the other hand in the substrain where selection for fluoroacetate resistance was discontinued, the level of resistance to dieldrin fell more gradually and stays now at approximately 1,000 fold of the original strain used for fluoroacetate selection. For lindane the picture is similar to that of dieldrin.

A ten fold increase in resistance to fluoroacetate was obtained after 25 generations of selection. The degree of fluoroacetate resistance then declined slowly, in spite of rigid selection procedures. After the 44th generation it rose again, regaining at the 65th generation the former 10 fold increase.

The fluoroacetate selected strains were completely susceptible to organo-phosphorus insecticides, such as parathion, malathion, and trichlorfon.

During the selection process it was noted that flies selected for fluoroacetate resistance could withstand longer periods of lack of water and food. The LD_{50} for the normal strain was 26 hours, and for the fluoroacetate selected strains 68 hours. The ability of the fluoroacetate selected strain to subsist without food or water remained also after 65 generations of selection.

The significant observation of this study is the high resistance which the fluoroacetate-selected strains developed against dieldrin, lindane, DDT and methoxychlor, although these strains had never been in contact with any of these insecticides

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GENETICS OF RESISTANCE TO INSECTICIDES IN *DROSOPHILA*

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(1) Genetic nature of resistance to DDT and Dieldrin in *D. melanogaster*.

The levels of both resistances of many strains collected from various localities were estimated by test papers and the expression of those resistances was assumed to be normally distributed in natural populations. A resistant strain from Hikone, Japan, collected in 1952, showed the highest resistance to both insecticides which has been evidently acquired before due to several years' selection by DDT.

(2) Chromosomal analysis of resistance to DDT and nicotine sulfate in *D. melanogaster* and *D. virilis*.

The Hikone strains of both species, an inbred line Canton-S and a marker strain having a recessive mutant gene on each autosome were crossed with each other. The resistance of F_1 and F_2 flies having various genotypes was estimated separately; the high resistance was found to be controlled by dominant genes on two autosomes of both species. From the fact that those two autosomes were thought to be homologous, the resistance was presumed to be a pre-adaptive character.

(3) Experimental analysis by using a method of population genetics.

Artificial populations were constructed with *D. melanogaster* flies, most of whose autosomes were substituted by susceptible ones, except for one resistant chromosome, and they were cultured continuously in DDT free environment for about two years. Their resistances to DDT gradually decreased. From the result, a major resistant gene in the genetic background lacking modifying polygenes would be disadvantageous to natural selection.

OUTSTANDING PROBLEMS IN THE GENETICS OF INSECTICIDE RESISTANCE

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If I had to make a thumb-nail sketch of the genetics of insecticide resistance, I would say something like this: "The inheritance of a considerable number of instances of insecticide resistance has been investigated by various workers and the results are fairly consistent. In almost all cases, resistance is inherited through normal Mendelian genes, usually a single pair, which may be dominant, intermediate or recessive in expression". While I believe most experts would not disagree with this statement, it must be admitted that the subject is more complex than it suggests and also that there are a few rather unsatisfactory loose ends. I want to deal with 5 matters of this type.

1. There is, by now, overwhelming evidence that resistant strains develop almost exclusively by the selection of pre-existing genes. At the same time, there are occasional reports of post-adaption which deserve investigation, either (*a*) in susceptible insects or (*b*) in resistant ones.

(*a*) Certain Russian workers, notably Derbeneva-Ukhova, have noted harmful effects of sub-lethal contacts with DDT on the ovaries of susceptible flies and claim that these accumulate and cause resistance. My colleagues, Dr. B. C. Fine and Mr. S. C. Srivastava, have investigated this possibility by treating normal flies with low, non-lethal doses of DDT and recording egg production as well as hatch. They found a slow increase in tolerance (up to $\times 2$ in F_7) followed by a decline; in short, no real evidence of post-adaption.

(*b*) Various workers have found that, if larvae of dieldrin-resistant strains were reared in dieldrin containing medium, the resulting adults were more resistant than normal (*Aedes aegypti* in A. W. A. Brown's department; *Musca domestica* at the Pest Infestation Laboratory and my own laboratory). Since the strains in all cases appeared to be homozygous for resistance, the enhancement of tolerance is difficult to explain and remains a puzzle.

2. As regards dominance, DDT resistance is variable, not only in different species of

mosquitoes (where it is either recessive or intermediate) but also in different strains of resistant houseflies, where it ranges from one extreme to the other. In contrast, dieldrin resistance is almost always inherited by genes of intermediate dominance. This was found in 5 strains of anopheline and 2 culicine mosquitoes, in houseflies and 2 blowflies, bugs, lice and cockroaches. Only recently have there been exceptions in 2 strains of *Anopheles gambiae*, showing full dominance. The resistance genetics of organo-phosphorus insecticides have been less investigated. The 4 cases available all show full dominance.

The following questions arise. Does the expression of dominance depend on separate genes modifying the expression of resistance? Alternatively, are the different levels of dominance due to the presence of different genes for a given type of resistance? It is indeed true that toxicological evidence suggests that dieldrin resistance is very uniform, whereas DDT resistance may be due to more than one mechanism.

It may be worth assembling some data concerning crosses between similar resistant strains from different sources, to see whether the genes were identical, allelic or non-allelic.

Probably identical: DDT-resistant *Aedes aegypti* strains from Malaya and Trinidad, tested in Prof. Brown's department. Dieldrin-resistant *Lucilia cuprina* from Australia and South Africa, tested in my department.

Allelic, but not identical: Dieldrin-resistant *Blattella germanica* from Germany and Texas, tested by Dr. Cochran.

Non-allelic (not reinforcing in F_1): DDT-resistant houseflies from Italy and Florida, tested by Prof. Milani. Also, probably, the dieldrin-resistant strains of *Anopheles gambiae* from Liberia and Nigeria, tested by Mr. Davidson.

Non-allelic (but reinforcing in F_1): Dieldrin-resistant strains of housefly tested by Prof. Milani.

3. Both in the laboratory and in the field, there is evidence that homozygous resistant strains are less viable than the other genotypes and, in the absence of selection, they tend to revert to the heterozygous condition. It is not clear why the homozygous form is less viable. Is it because of a harmful pleiotropic effect of the resistance gene? Alternatively, it has been suggested that subsidiary genes may be necessary, to accept the new gene into the genetic background. This is supported by the fact that (both in laboratory and in the field) prolonged selection for resistance tends, finally, to produce a more viable, stable homozygous strain. But this explanation does not seem to have been proved.

4. Cross resistance may be of two types. There is the invariable automatic resistance to two insecticides due to the fact that the same mechanism protects an insect from both of them. Another type of cross resistance may be an association of 2 distinct forms of resistance, such that selection for one sometimes causes increase in resistance for the other. An interesting anomalous case of this kind is the selection by o-p insecticides which has been reported as causing large increase in resistance to chlorinated insecticides (in houseflies); whereas the reverse relation does not hold. I would like to suggest a tentative explanation. Possibly the resistance to chlorinated insecticides confers a slight tolerance to o-p insecticides, whereas o-p resistance mechanisms give no protection at all to chlorinated compounds. (This is plausible, if we compare dieldrin resistance, which seems to be due to insensitivity at a vital site, with o-p resistance mechanisms, which are essentially de-toxifications.) Given this situation, selection by a chlorinated insecticide will finally produce chlorinated insecticide resistance and a *small* cross tolerance to o-p compounds; but it will not concentrate any o-p genes which may be present. On the other hand, selection with o-p insecticides may tend to concentrate genes for chlorinated resistance, by virtue of the slight o-p tolerance they provide. This would be spectacular, in a population containing several chlorinated resistance genes but with few or no genes for o-p resistance. Naturally, this hypothesis requires proof.

CYTOTAXONOMY

CHIRONOMUS TENTANS (DIPTERA): THE GIANT CHROMOSOMES AND TAXONOMIC DIVERGENCE

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If a closely related pair of species were to be traced back in time to the point where they were just starting in the process which is called speciation, they would have existed at this point as a pair of populations which differed in some respect, however difficult to recognise. If theory is not too wide of the mark, such populations must exist now in appreciable numbers, and it might at first sight appear to be a straightforward matter to study them in order to learn how species form. Unfortunately, differences between related populations will only occasionally be the criteria of incipient species. More often such differences will be the result of short-term adaptations, or may be purely environmentally induced. For any study to be of value, it is essential to be able to distinguish between these categories.

One character which is almost uniquely suited for such an investigation is the banding pattern of the giant chromosomes of dipterous larvae. These patterns are completely isolated from any environmental influence and so are subject to heritable variation only. Their complexity makes it unlikely that the patterns of different species would come to resemble each other by chance alone, and since the patterns are not used *as such* by the animal, they are unlikely to show convergences in different species as a consequence of adaptation to a common habitat.

Often homologous chromosomes within a single interbreeding group differ from each other by inverted regions, and, less often, in other features. Nearly always one type of homologue will be more common than the alternative, and this will be the obvious choice as a basic pattern with which others can be compared. In the same way, it is possible, usually by the criterion of numerical preponderance, to decide upon a single basic pattern which will serve for a large number of populations.

However, if the reference banding patterns of one population differ from those of another population by a large number of inverted regions, and if furthermore, the inversions by which they differ can be found individually and as heterozygotes in no existing population, this is fair evidence that the two populations in question are genetically isolated. If such differences are found between two groups of populations, such as between all those in one continent and all those in another, this is evidence that there is very much reduced migration between the continents.

Chironomus tentans occurs throughout the Holarctic Region. There is no difficulty at all in finding a single set of reference patterns for all the larvae found in Britain, Germany and Sweden. Similarly, there is a single set of reference patterns for all the larvae taken throughout Canada. However, these two sets of patterns differ; and differ by features possessed by *every* larva in each area. Chromosome 1 has a nucleolar organiser in Canada and U.S.A.; it has none in Europe. Chromosome 2 differs by a number of inversions which are found nowhere as heterozygotes. Chromosome 3 in Europe has a nucleolar organiser; in Canada and U.S.A. it has an additional band and no nucleolar organiser. Chromosome 4, the smallest, has the same reference pattern throughout.

The only population found in Alaska had chromosomes similar in nearly every respect to the *European*, not the Canadian, though a small number of features were of the Canadian type.

This evidence suggests, not, as might have been expected, that the barriers between North American and European populations were the Atlantic and Bering Strait, but rather the Atlantic and the ice cap of a previous Ice Age. The known dating of the interglacial periods makes it possible to estimate roughly how long it may take for a new species to evolve.

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HYBRIDISATION BETWEEN NORTH AND SOUTH AMERICAN *TROPISTERNUS* (COLEOPTERA: HYDROPHILIDAE)

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A melanic form of *Tropisternus collaris* (Fabricius) from Lake Ayapel in Colombia (South America), has been successfully crossed with specimens from the White River near Elnora, Indiana (U.S.A.). F_1 hybrids show high viability in survival of both larvae and adults. The color pattern of most hybrids closely resembles that of the Indiana parent presently considered to be *T. mexicanus striolatus* (LeConte) but a few show characteristics of *collaris*. Interaction of modifier genes is suspected. F_1 hybrids show high sterility. Translocations which interfere with meiosis may be present. Backcrosses show higher viability. Elements of the color pattern show some segregation but not random assortment. Three crosses of backcross individuals which resemble the South American parent to the South American form show even higher viability. All of the latter adults resemble the South American form, but there are some indications of intermediacy.

The following table summarises the results of the rearing of inbred lines and crosses in terms of fertility. AYA* indicates the South American form (*collaris*) and ELN* the Indiana form (*striolatus*):—

Fertility of Parent Strains and Crosses
(Sept. 1963 through May 1964)

	Strain or Cross	*No. of Females*	*Eggcases*	*Maximum no. Eggcases/Fem.*	*No. Eggcases Hatching*	*Maximum no. larvae/eggcase*	*Total no. Larvae*	*Adults Reared*	*% Larvae reared to Adults*
Inbred Lines	AYA+ × AYA+	7	55	23	52	42	929	103	11%
	ELN+ × ELN+	5	15	5	15	28	156	59	31
Crosses	AYA+ × ELN+	2	9	5	9	38	297	139	46
	ELN+ × AYA+	2	6	4	4	32	69	33	46
(*AYA* × *ELN*) × (*AYA* × *ELN*)		27	104	12	2	1	2	1	—
(*ELN* × *AYA*) × (*ELN* × *AYA*)		4	11	4	0	0	0	0	—
(*AYA* × *ELN*) × AYA+		20	133	20	37	8	129	24	18
(*ELN* × *AYA*) × AYA+		1	3	3	3	5	12	5	41
(*AYA* × *ELN*) × AYA+ × AYA+		3	14	8	14	24	242	127	52

Female parent in each case given first.

It is concluded from these experiments and the examination of the few specimens available from intermediate areas that *T. collaris* interbreeds with *T. mexicanus* in Panama and probably in northern Colombia. *Tropisternus collaris* (Fabricius) is therefore considered to include *T. mexicanus* (Castelnau) and its subspecies *striolatus* (LeConte), *viridis* Young & Spangler, and *proximus* Sharp. *T. paranamus* Sharp and *T. lepidus* (Castelnau) are also considered to be subspecies of *collaris*. Other geographically localised populations of *collaris* probably also represent subspecies but have not yet been described.

CYTOLOGY AND CYTOTAXONOMY OF MOSQUITOES

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Past and current work on the cytology and cytotaxonomy of mosquitoes may be divided into three areas. First, the study of karyotypes and mitotic stages; second, work with salivary gland chromosomes; and third, investigations of spermatogenesis and the mature sperm.

Kitzmiller (4) has given an excellent summary of much of the previous work; he lists an extensive bibliography, and has made suggestions for future investigations. Except for a few general remarks, the present paper and listed references will emphasize work done and articles published after Kitzmiller's paper was completed.

Work on karyotypes and mitotic stages may be briefly summarised as follows. The karyotypes of approximately 75 species of mosquitoes are now known. In all cases $2n = 6$. Minor differences exist among the karyotypes of non-anopheline mosquitoes, but the only really distinctive ones known occur in species of *Anopheles.* Three distinctive karyotypes occur in this genus, and karotypes have been used in determining relationships among species. With respect to the study of mitotic stages, satellites have been found in prophase in some species which could prove quite significant. The search for distinctive karyotypes should continue, and mitotic stages other than metaphase should be investigated more fully.

Salivary chromosome maps are now available for several species of *Anopheles*, and most species of this genus that have been studied can be identified by the patterns of the salivary gland chromosomes. Continued studies of salivary gland chromosomes should contribute greatly to our knowledge of relationships and evolutionary mechanisms among the various groups of mosquitoes.

One of the most recent studies of the meiosis part of spermatogenesis is that of Akstein (1) who worked with *Aedes aegypti.* In a recent paper (3) a description is given of meiosis in *Culiseta* (= *Theobaldia*) *inornata.* The principal differences found in this species compared with studies on other species (*A. aegypti*, *Anopheles stephensi*, and *Culex quinquefasciatus*) is the presence of a prometaphase stretch in prophase I, and the polarisation of the chromosome arms toward one side of the cell in prophase II. These phenomena have not previously been suggested in mosquitoes.

Spermateliosis or spermiogenesis has been almost completely neglected in mosquitoes. The writers have recently obtained excellent results by mounting testes in saline and studying them with the phase contrast microscope. No species have been completely worked out, but *Aedes aegypti*, *Culiseta inornata*, *Culex quinquefasciatus* and *Orthopodomyia* sp. have been examined. The method of development of the tail filaments is an outstanding feature of this species. As the filaments elongate, they encircle the inside of the cell and surround the nucleus from one to several times. As development proceeds, the tail becomes straight by "unwinding". The straightening of the tail is accompanied by a rotation of the nucleus within the cell until it is in line with the tail. Indications are that details of development vary among the different species.

Aceto-orcein or 70% acetic acid added to mature sperm in saline on a slide causes the filaments that comprise the tail to unwind, and in high concentration, may cause the tail to disintegrate completely. The sperm heads are relatively unaffected.

The tail of *Culiseta inornata* apparently consists of three filaments at the phase contrast level of resolution. One of these is straight whereas the other two are sinuated. The two outer filaments unwind as the acid or stain comes in contact with the tail. A photograph of the effects of aceto-orcein on the tail of the sperm of *Culiseta inornata* was recently published (2). Preliminary studies suggest that the structure of the tails of sperm vary in different species of mosquitoes. The use of aceto-orcein or acetic acid as noted above is an excellent method for studying the head or head complex (probably also includes the middlepiece) of mature sperm. The use of these materials causes differentiation of the head complex and tail or axial filament to be relatively easy, whereas this is often difficult in untreated sperm.

By using this method, the sperm heads of *Aedes aegypti*, *Culiseta inornata*, *Culex quinquefasciatus* and *Orthopodomyia* sp. have been studied. The head of *C. quinquefasciatus* is the shortest, being only

one-fourth to one-third the length of the others. The sperm head of *Orthopodomyia* is next in length, being somewhat shorter than the other two. It also has a small rounded enlargement at the base. The sperm heads of *A. aegypti* and *C. inornata* are near the same length. That of *A. aegypti* is flared on both sides at the base, whereas, the sperm head of *C. inornata* is only slightly enlarged on one side, and the end is angularly truncate.

It is hoped that these reported results will encourage other investigators to apply these or similar techniques to other species of mosquitoes and other insects. Possibilities for investigations of the fine structure of sperm are suggested by a recent publication of Núñez (5).

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PARTHENOGENESIS

COLOUR PATTERN POLYMORPHISM LINKED WITH INCIPIENT SPECIATION IN *TENTHREDO ACERRIMA* BENSON (HYMENOPTERA, TENTHREDINIDAE), AND SPECIATION IN SAWFLIES

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Larval polymorphism in this single brooded sawfly was reported by Waterhouse and Sanderson (3).

Larval colour patterns. In the south of England larval types are distinguishable in late instars by trunk segment markings, simplified diagrams of which are illustrated in Fig. 1. Shading denotes areas prominently dark against a green background. Fig. 1A is a dark type with full pigmentation. The supra-spiracular line markings take the form of a light mid-dorsal area and an interrupted, blotchy supra-spiracular stripe with the intervening area moderately and uniformly pigmented. Two more marks occur at the base of the prolegs. Fig. 1B shows a light or spotted type where pigmentation is as shown or reduced. There may be only a single spot above the spiracle. Figs. 1C and D are classified as intermediates.

In Scotland only the spotted type B is seen.

Crossing of English and Scots forms. If an English female, arrhenotokously producing A type larvae is mated with a Scots male the subsequent brood will comprise further A type male larvae and some female larvae similar to type C.

A reciprocal cross using an English male, bred from an A type larva produces female heterozygotes as before but with the anterior segments usually showing more colouring as in Fig. 1D. Male larvae are of course of type B.

The F_2 brood, achieved by rearing the heterozygotes parthenogenetically next year, segregates in approximately equal number of type A and B larvae with reduced pigment intensity.

It would appear that few genes are involved and those responsible for the extra pigmentation of A type larvae are partially suppressed in the heterozygotes. Variation suggests either the importance of additive gene effects or the influence of different genotypes.

These north/south crosses thus explain the simulated continuous variation in the south of England where, due to parthenogenesis, either light or dark forms can occur separately or along with heterozygotes.

Speciation. English and Scots larvae differ in their mean life history periods, colour intensity and polymorphism whilst the adults not infrequently fail to produce heterozygotes after pairing. This suggests incipient speciation.

Maxwell (1) and earlier conversation with this author first drew attention to the likelihood of the above colour pattern genetics being found elsewhere in the Tenthredinidae. It is therefore all the more interesting that Moens and Atwood (2) have shown a colour pattern inheritance in *Neodiprion pratti* Dyar in Canada which so closely resembles the one described above that the same account might almost serve for both. However although they record

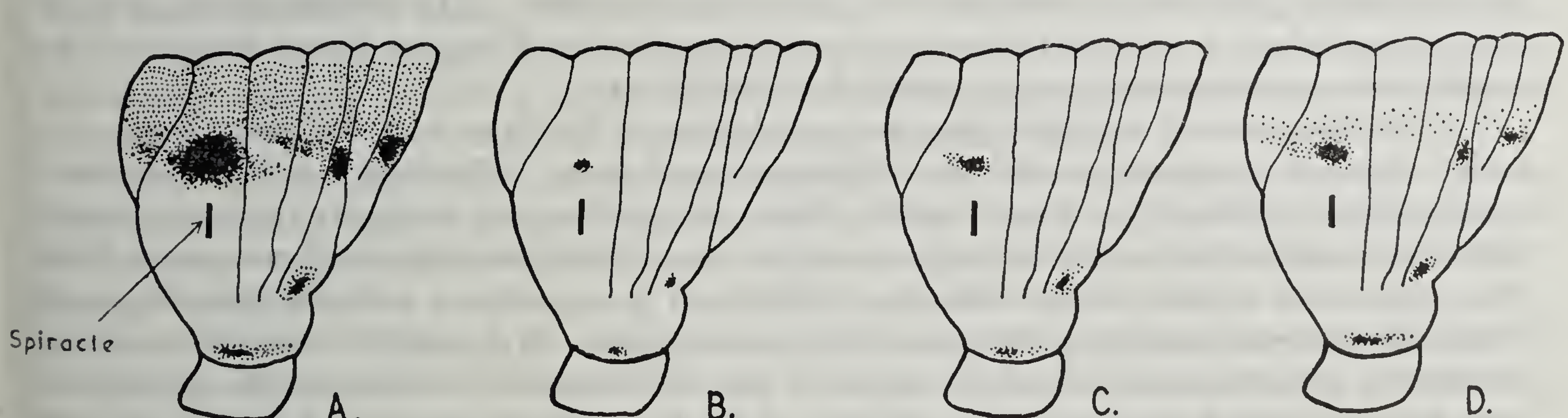

Fig. 1. Simplified trunk segment diagrams in *Tenthredo acerrima*

both striped and spotted forms in varying proportions in different areas, they state that neither form exists in isolation.

The similarity of the pattern polymorphism in these two fairly unrelated genera suggests that an almost identical speciation mechanism may have been exploited many times by sawflies. The *Tenthredopsis* complex may have arisen in this way since the adjacent species *nassata* L. and *litterata* Geoffr. possess unicolorous and striped larvae respectively, whilst the latter species itself presents two larval colour forms of the same pattern.

I wish to record thanks to my friend and colleague Mr. A. T. Baxter of Ashtree Gate, Bledlow Ridge, Bucks., for enthusiastic help and shrewd advice.

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PARTHENOGENESIS IN APHIDS

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Parthenogenesis in Aphids is not ameiotic as was formerly believed. A peculiar type of meiosis (endomeiosis) was detected in parthenogenetic oogenesis. The origin of the variability within the parthenogenetic lines of Aphids can now be interpreted as the result of crossing-over taking place during parthenogenetic oogenesis. This was demonstrated with the following experiment: five stem mothers of *Brevicoryne brassicae* (a, b, c, d, e) were put in the same thermostat and each of them was kept isolated on a small leaf of *Brassica oleracea*. Environmental conditions were regulated in order to obtain the production of sexuales and these conditions were kept steady for the whole duration of the experiments. No further parthenogenetic females were produced in the 3rd, the 5th and the 4th generation of the a, b, c strains respectively. In the 3rd generation of strain d, only two parthenogenetic females were produced and they gave rise at the 4th generation to a higher number of parthenogenetic daughters. These increased more and more in the next generations. Strain e showed a similar behaviour. It is possible therefore to select genotypes which favour parthenogenetic reproduction even in environmental conditions which are not favourable to its expression. The existence of this genetic variability within parthenogenetic lines is evidently due to endomeiosis.

A racial variability concerning the determination of the heterogonic cycle within species of Aphids can therefore be assumed on the basis of the above results. Many species in fact show populations which reproduce constantly by parthenogenesis in regions with hot climate, while in other regions with cold winters sexuales occur. According to the results described above, these differences in the reproductive cycle are to be considered not as exclusively phenotypic but as depending also on the existence of racial and therefore of genetic variability.

This interpretation was verified in populations of *B. brassicae* collected from various localities having different climates: cold temperate climate at different altitudes and mediterranean climate. Fifty parthenogenetic females of each population were isolated on cabbage leaves and put in the same thermostat regulated for obtaining sexual forms. Almost all the populations of the cold temperate climate show no parthenogenetic females in the 4th or 5th generation. In one population however three parthenogenetic females which appeared at the 5th generation gave rise by selection to a parthenogenetic line. The mediterranean populations instead show a marked tendency to parthenogenesis and the conditions favourable for amphigonic reproduction exerted practically no influence.

It is demonstrated therefore that the populations of localities with different climate are unlike in genetic composition and form different sexual races. The higher or lower tendency to amphigony is directly in relation with climate of a region, but evidently the environment influences populations having multiple genotypes even within the single parthenogenetic lines. The populations of different localities react differently in accordance with the reaction norms of the different sex genotypes composing their genic pools. It is possible therefore to obtain constantly parthenogenetic lines, in spite of the unfavourable environmental conditions, from strains in which amphigony occurs because the original sex variability has been reduced by selection.

GENETICAL CONTROL OF NOXIOUS INSECTS

THE STERILITY PRINCIPLE OF INSECT POPULATION CONTROL

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As a working hypothesis, it can be assumed that if a sufficient number of sexually competitive but sterile insects are introduced into the environment to cause a downward trend in the population of an insect species, and if such releases are maintained over a period of several generations, the inevitable result will be the elimination of the population.

Because of the large number of individual insects present and the large areas generally involved in well established populations, it will not be economically feasible to employ this procedure alone for meeting most of our insect problems. However, there are many circumstances where the system, integrated with other control methods, should be of great value in meeting important insect problems.

Current methods of pest control, involving outright destruction of organisms, are efficient when the pest population is high, but inefficient when the pest population is low. In contrast, the sterile insect release method is generally inefficient when the pest population is high but highly efficient when it is low. Thus, by integrating the two systems, we have for exploitation an approach to pest control that offers many possibilities, because such integrated system is more effective than either system employed alone.

The Table shows the characteristic trends of insect populations subjected to different systems of control.

It should be noted that insecticide treatments at the 90 per cent level (Column 2) would be required for 18 generations in order to achieve theoretical elimination of the population. It should also be noted that as the population declines, insecticide treatments become less efficient each generation in terms of numbers of insects killed. If insects in the natural population were appropriately sterilised instead of killed, the sterility treatment of the 90 per cent level would affect population trends as shown in Column 3. Theoretically, complete elimination of the population would be achieved if treatments were made for 5 generations.

The release rate of 9,000,000 fully competitive sterile insects in each generation would theoretically have the effect shown in Column 4, and theoretical elimination would be achieved in the F_4 generation by the use of 45,000,000 sterile insects.

The last column shows the results of a combined programme of insecticides and sterile insect release. Theoretically, the integrated system would be by far the most efficient, requiring insecticide treatment for one generation only plus the release of 4,000,000 sterile insects.

The sterile insect release method has been employed successfully for the elimination of the screw-worm from Florida and other South-eastern States. The procedure is now being applied for the control of this livestock pest in the south-western part of the country.

In spite of unexpected long distance dispersal of the insects, the program in the South-west has been highly successful. Sterile fly releases are being made at rates ranging up to 140 million per week in an area involving about 200,000 square miles. The level of control now being obtained is about 99·9%.

Research by investigators with the U.S. Department of Agriculture has shown that the sterile insect release method is highly effective in eliminating populations of certain species of tropical fruit flies. These insects are polygamous in mating habits.

Investigations are under way by entomologists in the U.S.A., Canada, Australia and in other countries to explore the sterile insect method for the control or elimination of other major insect pests. In addition to tropical fruit flies, encouraging results are indicated in the investigations on such insects as the codling moth, pink bollworm moth, tobacco hornworm moth, and the boll weevil. Through the establishment of hypothetical models the writer has attempted to appraise the potential role that sterile insect releases might play in eliminating populations of various important insects.

Two ways of employing sterile male releases have been considered for controlling popula-

tions of tsetse flies. One way involves the use of sterile male releases alone to eliminate a low density population. The other method involves the application of a single insecticide mist spray treatment to reduce the natural adult population followed by the sustained release of sterile males.

On the basis of these studies, the writer has estimated that the release of about 1,700 fully competitive sterile male tsetse flies per square mile during a period of about one year should eliminate a population of tsetse flies that initially averages about 200 plus per square mile.

Methods of rearing tsetse flies in large numbers have not been perfected, but there is reason to believe that mass rearing methods could be developed. If it were possible to rear tsetse flies in large numbers at a cost level of 5¢ for each male, and if the estimated requirements of about 1,700 sterile males would eliminate low level natural populations, the cost of 85°° for the sterile insects would compare favourably with the estimated cost of 500°° per square mile that probably would be required to eliminate such populations by the use of residual insecticides.

The use of sterile males alone may be practical and economical for eliminating low level populations. However, the greatest potential for the sterile male technique will no doubt be realised when the system is used against high populations in combination with the minimum use of insecticides. A study of hypothetical populations averaging 1,000 tsetse flies per square mile, suggests that complete elimination of such populations should result from a single insecticide application followed by the release of about 1,500 sterile males during the next 6-12 months. Mist spray treatments alone would probably require 6-8 treatments to achieve complete elimination.

Much research will be required on each insect species to determine the feasibility of its control or eradication by the use of sterile organisms. However, the principle offers such great potential, it would seem desirable for scientists engaged in research on major pests, both invertebrate and vertebrate, to devote more research to investigate fully this approach.

TABLE SHOWING THE RELATIVE TRENDS OF HYPOTHETICAL INSECT POPULATIONS SUBJECTED TO DIFFERENT SYSTEMS OF CONTROL

Generation	*Uncontrolled population* *	*Insecticide treatments (90% kill each generation)*	*Chemosterilant treatments (90% sterility each generation)*	*Sterile insect releases (9,000,000 each generation)*	*Integrated programme of insecticides and sterile insect releases*
	1,000,000	1,000,000	1,000,000	1,000,000	1,000,000
F_1	5,000,000	500,000	50,000	500,000	45,450
F_2	25,000,000	250,000	2,500	131,625	9,880
F_3	125,000,000	125,000	125	9,540	485
F_4	Same	62,500	6	50	0
F_5	Same	31,250	0	0	
F_6	Same	15,625			
F_7	Same	7,812			
F_8	Same	3,906			
Total requirements for theoretical elimination of populations		Treatments for 18 generations	Treatments for 5 generations	45,000,000 sterile insects	Insecticide treatments for 1 generation plus 4,000,000 sterile insects

* It is assumed that the uncontrolled populations increase at a 5-fold rate until the maximum density for the environment is reached, which is assumed to be 125,000,000.

POSSIBLE CAUSES OF FAILURE IN A FIELD TEST OF THE "STERILE MALES" METHOD OF CONTROL

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Lucilia sericata Mg. is a strong flying Calliphorine fly which occurs in low density, (<5 per acre), in Britain. It can be reared easily in the laboratory in large numbers. In its larval stage it can be an ectoparasite of sheep; the adult is not a pest.

Control of this species by the method of release of sterilised males was tried (2). After release of large numbers of γ-radiation-sterilised *L. sericata* into a small, apparently isolated, population for two seasons, reliable estimates showed that the population had not even been reduced. The present paper looks at various aspects of the test for any evidence of possible causes of failure.

1. Donnelly (1) showed that, provided one third of the pupation time had elapsed at time of radiation, *L. sericata* will survive γ-doses of up to 24,000 rep.

Both males and females are sterilised by doses of 4,500 rep and above. Material for release was treated with 6,000 or 7,000 rep, at which dose adult longevity was reduced to 60% of normal. Sterility assessments were based on seven successive tests in which 300 to 500 pupae were subjected to each of the doses tried. 100 to 150 of the surviving adults were then subjected to fertility tests by caging each sex separately with normal, virgin flies of the opposite sex and measuring the fertile egg output of the cage. These tests were supplemented by a further four confirmatory tests and by tests conducted on samples from actual release batches.

Mates of males irradiated with 6,000 rep and over gave only 5 egg masses which showed residual fertility. In these, no more than 10 viable eggs per cluster were obtained. It is not thought that so few larvae would successfully establish as a feeding population.

2. Laboratory tests showed that sterilised males did not recover fertility during their lifetime.

Material for release was packed into small bulk for more uniform radiation doses, and was so enclosed for a 60 hour transit period. Although it may have been subjected to CO_2 tensions of 3-5%, there was no evidence that this had affected either viability or radiation sensitivity of the material.

3. Holy Island, where the test was conducted, is some one mile square—agricultural land with a small village, and having a small peninsular extension of sand dunes of $\frac{1}{2}$ to $\frac{3}{4}$ sq. mile. The estimated population of *L. sericata* was in the order of 2,000.

An initial release of 20,000 followed by weekly replacements of 10,000 should have maintained a sterile:fertile ratio of 10:1. While these amounts were achieved, an unknown and possibly serious loss of effective sterile population may have occurred due to:

(*a*) serious depredation at emergence while large numbers of newly emerged flies were aggregated at the release sites;

(*b*) loss of viability inherent in laboratory strains under field conditions;

(*c*) very low emergence rates in released material during the first season especially;

(*d*) vulnerability of young material to extreme weather conditions.

4. Specially conducted tests by release and recapture of large numbers of code-marked adults showed:

(*a*) the *L. sericata* population of Holy Island was isolated from that of the mainland—no immigration on to the island occurred;

(*b*) there was adequate dispersal of adults over the island.

5. Sterilised males were capable of copulation and were as ready as normal males to effect one copulation with a fertile female. However, there was evidence that the sterile male was not as effective as the normal in achieving a second copulation, and was incapable of a third. Normal males, on the other hand, average at least six and are sometimes capable of up to twelve copulations.

The earliest encounter of a sterile male with a female is more likely to be with one of his own release batch rather than a native, because of the method of releasing in large batches of pupae. This absorption of the total potency of a sterile male by a single sterile female would have been reduced in its effect, due to the fact that neither sex can mate within their first three

adult days—thus allowing time for some dispersal before copulation.

In this species, mating does not prevent the female accepting a second mate. Progeny of a female following a second mating are all from the second male. Thus, sterile males of *L. sericata* would be unable to "block" the subsequent fertility of any normal female mates.

6. Special laboratory tests demonstrated that, in laboratory strains of this species, assortative mating does not occur.

No clear-cut cause of failure has so far been demonstrated. Examination of the evidence to date shows that, in the sector of release and maintenance of adequate numbers of adequately viable, sterile, individuals, serious impediments to the success of the method may have existed.

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THE GAMMA IRRADIATION OF *GLOSSINA* PUPARIAL STAGES AND CONTROL

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In considering the application of this technique of control by release of sterilised males, to the tsetse fly (*Glossina*), it is first necessary to recapitulate the basic facts concerning the reproduction of tsetse flies. Single eggs mature, one at a time, in each of the two ovaries alternately, and pass into the uterus, in which the whole of the development of the larvae takes place. This is followed by a long pupal period, passed inside the skin of the third-instar larva, which has hardened after the extrusion of the larva from the uterus. From this case, the puparium, the adult fly emerges, after a short quiescent period as a pharate adult. The whole developmental cycle of *Glossina*, from emergence of the female from the puparium to emergence of its first offspring from the puparium, takes about 45 days at 24°C., the optimal temperature for development of the puparial stages, with a minimum of about 30 days at 31°C. (the highest temperature at which this development can be successfully completed) and a maximum of about 76 days at 17°C. (the lowest temperature at which development can be completed). The reproductive cycle of the tsetse is, therefore, a slow one, and the success of this insect in surviving is only achieved by its elimination of active larval stages living in the open and exposed to all the hazards that cause so great a mortality in the developmental stages of the house-fly (*Musca domestica*), the screw-worm fly (*Callitroga hominivorax*) and the mosquito.

Between April and September, 1956, puparial stages of *Glossina morsitans* Westw., collected in Tanganyika, were sent by air to London and then subjected to γ-radiation from an activated cobalt source by the Technological Irradiation Group of the Isotope Division of the Atomic Energy Research Establishment at Harwell. The γ-radiation was applied at a rate of 6,000 röntgens per hour or, in some experiments, per minute. The irradiated pupae, with untreated ones, were then maintained at the London School of Hygiene and Tropical Medicine, their viability, and the length of life of the flies that emerged from them and the fertility of these flies being observed. Dissection of samples shortly after their arrival in London showed that, in most of the puparia, a third or more of the life of the puparial stages had been completed, so that the individuals irradiated were all in the pupal or pharate adult stage, and were for the most part pupae that had completed nearly half their development.

The number of flies emerging from the puparia was not affected by irradiation at doses of 3,000, 6,000 or 12,000 rep, given at 6,000 r. per hour, but it was halved by a dose of 30,000 rep, given at 6,000 r. per minute. There was no impairment of the vigour of the males that had been subjected to the dose of 6,000 rep, as shown by their ability to compete successfully for females with untreated males; however, their length of life was about halved. Observation of the routine matings showed that males treated at this dose mated just as readily as the untreated ones, and males were observed to couple with the females from 10 to 91 days after irradiation had been effected.

The effect of the 6,000 rep dose on the males could only be tested by observation of their ability to fertilise untreated females, since the testes of the treated males presented a completely

normal appearance, and the spermathecae of the females mated with them showed the clouded appearance, due to the presence of sperm, typical of females mated with normal males. The ability of the male to fertilise the female was not, however, easy to assess, since, under laboratory conditions, females mated with normal males do not always produce larvae. This failure is due to the effect of captivity on the females rather than on the males; in captivity the delicate timing of the feeds relative to the ovarian cycle, necessary for maintenance of normal reproduction, is upset. In the assessment of the male fertility allowance therefore had to be made for this, and it was concluded that the percentage of matings between the untreated females and the irradiated males that result in the production of larvae is likely to be about 20. This conclusion was based on the results of 45 matings between the treated males and untreated females and 57 pairs of the untreated flies. However, the six females so mated that produced pupae produced only about half the number produced by females mated with normal males. It would therefore appear likely that this residual fertility of the treated males of 20 per cent. is higher than would obtain in practice, which might well be nearer 10 per cent.

However, two considerations that make it difficult to apply this technique to *Glossina* must be noted. The first is that this insect seems to be rather less susceptible to γ-radiation than the screw-worm fly. It is possible, however, that a greater degree of sterilisation might be effected by treatment with repeated small doses of γ-radiation aggregating to the same total dose; in other insects, this has been shown to result in more complete sterilisation without shortening the length of life. The second difficulty lies in the very slow rate of reproduction in *Glossina*, to which I have already drawn attention. This makes it improbable that mass production of tsetse in their puparial stages can be achieved with such brilliant success as with the screw-worm fly in Florida. There is, however, another alternative that I consider to be more likely to lead to success, the use of collected wild puparia for irradiation. It seems to me unlikely that this technique of control by release of sterilised males will be used on so large a scale that there will not be untapped reservoirs of wild puparia accessible.

I consider the following points urgently need further investigation:—

1. Whether thed egree of sterilisation of *Glossina* can be increased, without decreasing the length of life of the male, by use of repeated small doses of γ-radiation;
2. Confirmation that any residual fertility of the males that may remain, after the maximum sterilisation possible without undue decrease in the length of life of the male, will result in only a reduced female productivity;
3. Confirmation of a complete, or nearly complete, sterilising effect on the female;
4. Determination of the stage of puparial development at which irradiation (*a*) has the greatest sterilising effect, on both sexes, and (*b*) has the least effect in shortening the life of the male.
5. Exploration of the effect of doses below those needed for sterilisation, to determine whether dominant lethal genes may be produced in F_1 and F_2 generations.

CYTOGENETICS OF CHEMOSTERILANT-INDUCED STERILITY IN THE MOSQUITO *AEDES AEGYPTI* (L.)

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Considerable work has been done in the last few years on chemical sterilization of insects. However, the emphasis of this work has mostly been on screening a variety of chemical compounds as effective chemosterilants. Relatively small effort has been expended in studying some of the basic biological effects of chemosterilants and the detailed mechanisms by which they interfere with insect reproduction.

Work reported herein was undertaken to study the cytogenetic basis of chemosterilization in the yellow-fever mosquito, *Aedes aegypti*. Effects of a commonly used chemosterilant, apholate, on the somatic chromosomes and on the development of the reproductive tissues of this species were investigated.

Two to four days old larvae of *Aedes aegypti* were reared until pupation in a solution of 10-15 ppm apholate in tap water. Mitotic chromosomes were studied from squash preparations of fourth instar larval brains. At regular intervals ovaries from mosquitoes of known ages were dissected. Some dissections of testes from 8-9 day old males were also made.

The normal karyotype of *Aedes aegypti* consists of three pairs of rather large chromosomes which are individually recognisable. Apholate induced numerous aberrations in these chromosomes by virtue of its ability to break and physiologically modify them. Among the different aberrations observed were stickiness, deletions, ring chromosomes, dicentric chromosomes and anaphase bridges. Besides, apholate induced somatic polyploidy in some brain cells. It may also interfere with normal replication of the chromosomes. Induction of similar chromosomal aberrations in developing gametes would be expected to result in dominant lethality.

In the females, 15 ppm apholate induced almost complete infecundity. This resulted from an inhibition of oogonial development. The follicles in the treated females remained underdeveloped and sooner or later underwent complete degeneration. In some of these follicles a distinction into the nurse cells and an oocyte never took place. In others a complete breakdown of the follicular epithelium, nurse cells and oocytes was observed. Rarely, one or more follicles completed development in the treated females. Many of the eggs so laid, however, failed to hatch after insemination with normal males.

The size of the testes in 9-day-old treated males was not greatly different from those of 8-day-old untreated males. Nevertheless, the treated males appeared to be less fecund. Although motile sperms were produced by these males, hatchability of the normal eggs presumably after fertilisation with these sperms, was greatly reduced.

In conclusion, these studies have shown that chemosterilants may inhibit and completely prevent the production of gametes in insects (infecundity). When the gametes are produced after chemical treatment the so called sexual sterility probably results from the induction of gross chromosomal aberrations (dominant lethality) in sperms and ova.

Details of this work will appear in *Cytologia*, 29, (1964) and *Biological Bulletin*, 126, (1964).

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GENETICS OF BEHAVIOUR

SOME BEHAVIOURAL SELECTION EXPERIMENTS WITH *DROSOPHILA* (DIPTERA)

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My colleagues and I have been using selection as a method for "dissecting apart" some aspects of the behaviour of both *D. melanogaster* and *D. simulans*. Our primary interest has been behavioural and in no case have we carried genetical analysis very far.

The initial experiment (3) showed that the "Pacific" stock of *melanogaster* was highly variable for genes affecting the speed with which pairs mate when mature virgin flies brought together. The heritability of mating speed as measured by the rate of divergence between lines selected for fast and slow speeds is about 0·3. The character is obviously a highly complex one and it is possible to alter it in many ways. Here one of the main results of selection was to change the "general activity" of the flies such that the fast-mating lines were sluggish in all but sexual responses, whilst the slow-mating flies were hyper-responsive to any disturbance. Thus two aspects of mating speed, which we may call for short, "sexual" and "general" activity, have been separated. In wild populations they are both held at a compromise level by natural selection. The independence of sexual and general activity was further demonstrated by a second experiment (4). Here, following selection for slow mating speed in males alone, low sexual activity became associated with low general activity; a result which is similar to, but in this case certainly not due to inbreeding depression.

Our commonest estimate of general activity has been to introduce flies singly into a small arena, marked off in squares, and to count the number of squares entered within a short period, varying in different tests from 1 to 5 minutes. Recently Hobson (2), using a parent/offspring regression method, has estimated the heritability of this character in the "Pacific" stock of *melanogaster* as $0{\cdot}53 \pm 0{\cdot}077$. This rather high value taken together with high between-fly variance might indicate that the genes responsible have low selective values in this population. In view of the characteristic activity differences found between related species, this is probably a result of some hundreds of generations of domestication. Ewing (1) has been able to separate out, by selection, some of the factors contributing to general activity. Components we may tentatively label as "exploration" and "responsiveness to the proximity of other flies" are involved, among others.

Current work is concerned with the relationship between light, activity and mating speed. Within the *melanogaster* species group there is one species—*auraria*—which never mates in the absence of light, some, such as *melanogaster* itself, which are little affected in the dark, and others which are intermediate. Selection for "light dependence" and "light independence" in *simulans*, an intermediate species, is proceeding. Two lines of light dependent flies have been developed which are markedly slower to mate in the absence of light than unselected controls. Preliminary analysis indicates that the behaviour of both sexes has been affected and that the sexual responsiveness of males is reduced in the dark whilst unaffected in the light. These lines should prove useful material for an investigation of the relative roles of specific and non-specific visual stimulation in evoking activity.

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SELECTION FOR EXPLORATORY ACTIVITY AND ITS EFFECTS ON OTHER ASPECTS OF BEHAVIOUR IN *DROSOPHILA* (DIPTERA)

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Spontaneous activity, though difficult to define adequately, is an important concept since it may well prove fundamental to many more complex types of behaviour. In addition it is known that activity levels may vary from species to species and it is not difficult to imagine ways in which this could be of adaptive value. There have been few studies on the inheritance of exploratory activity using the method of selective breeding, and of these only Ewing (2) has used insects. Ewing's first experiment used a mass screening technique and although selection was brought about, subsequent checks showed this to be for "reactivity". A second method where insects were measured individually also produced a response to selection, though again not for activity but for a response to a specific part of his apparatus. Ewing concluded that his experiments had selected for a "claustrophobic" effect.

Materials and Methods. The flies used were from a heterogeneous stock of wild type *D. melanogaster.* They were reared at a temperature of 25° ± 1°C and on a light/dark cycle of 12 hours. All the measurements were made on individuals at 2-3 days of age, at the rearing temperature and at the same time of day. The animals were on an *ad libitum* feeding schedule until one hour before the test began when they were deprived of food but given water, this reduces the possibility of differences being a function of a diurnal rhythm of activity (1).

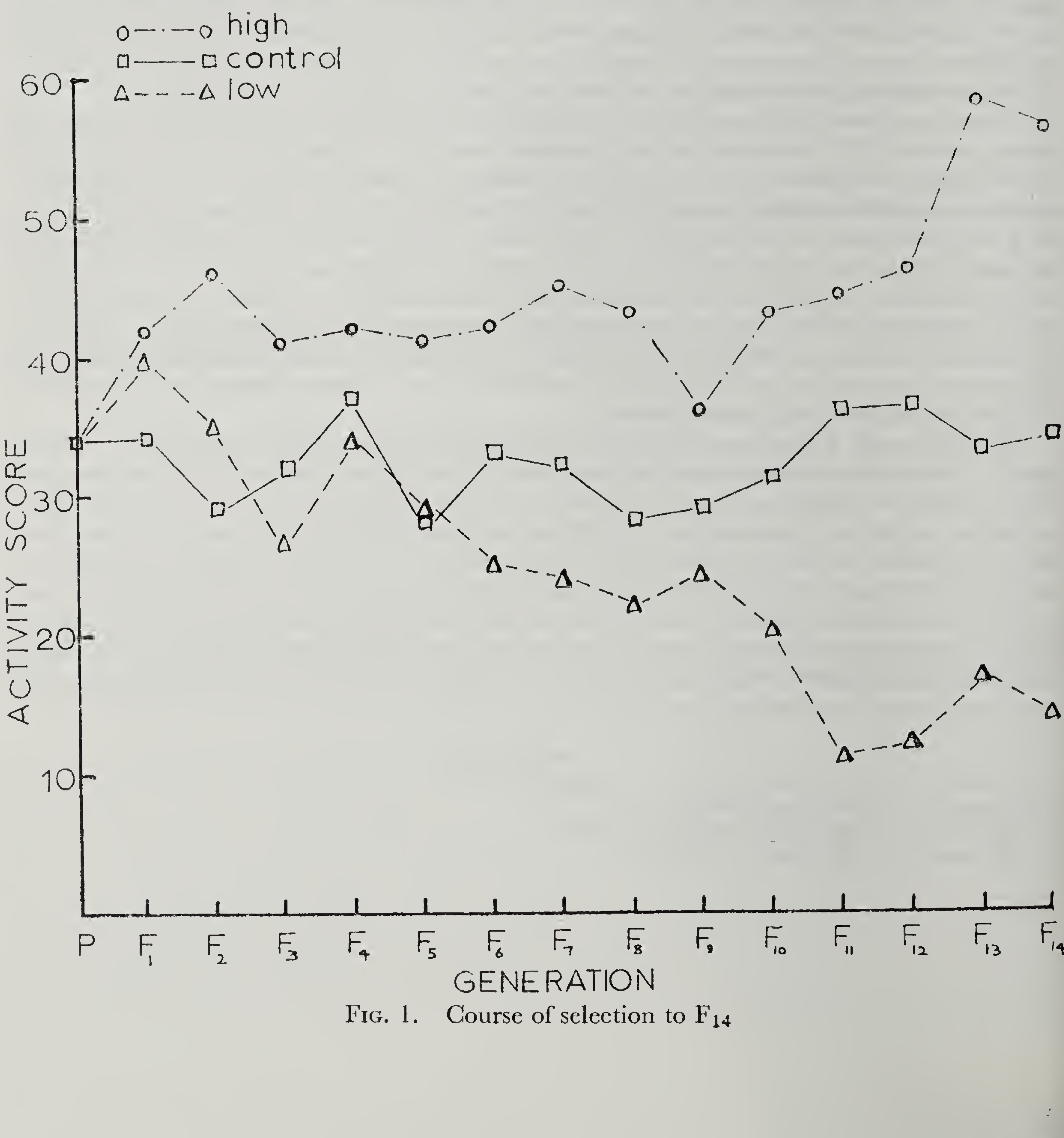
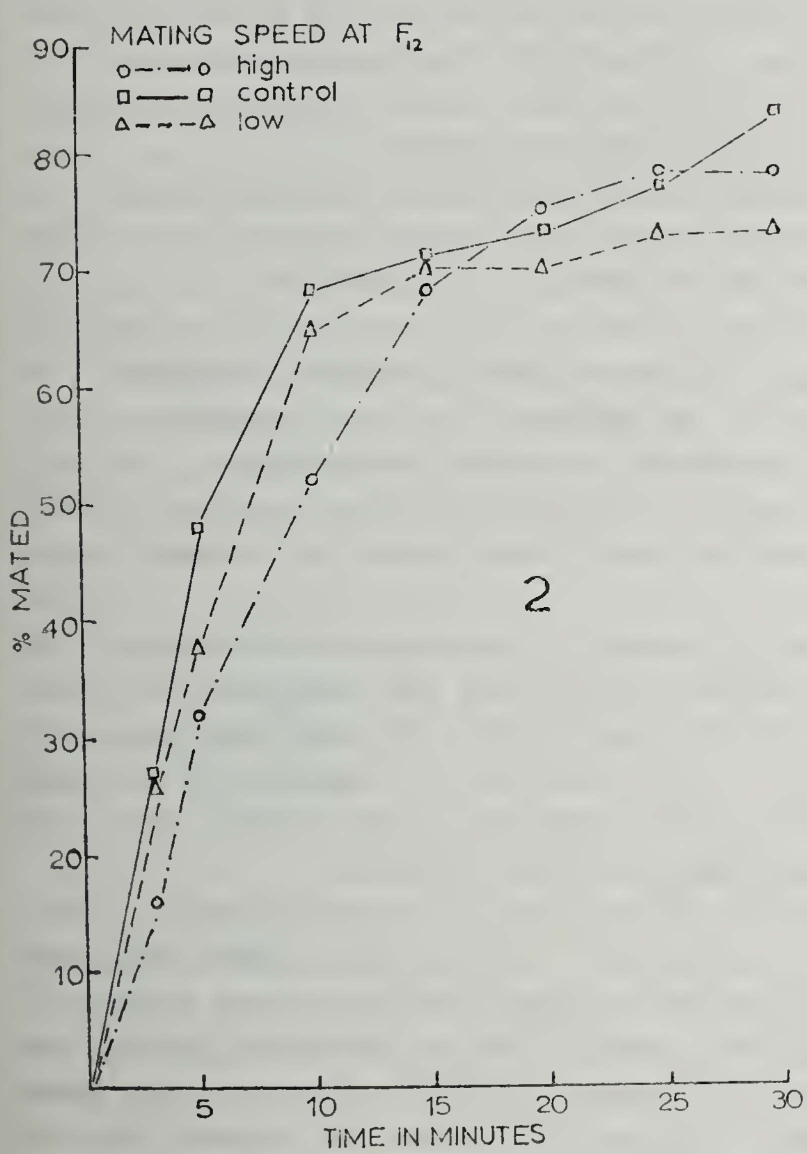


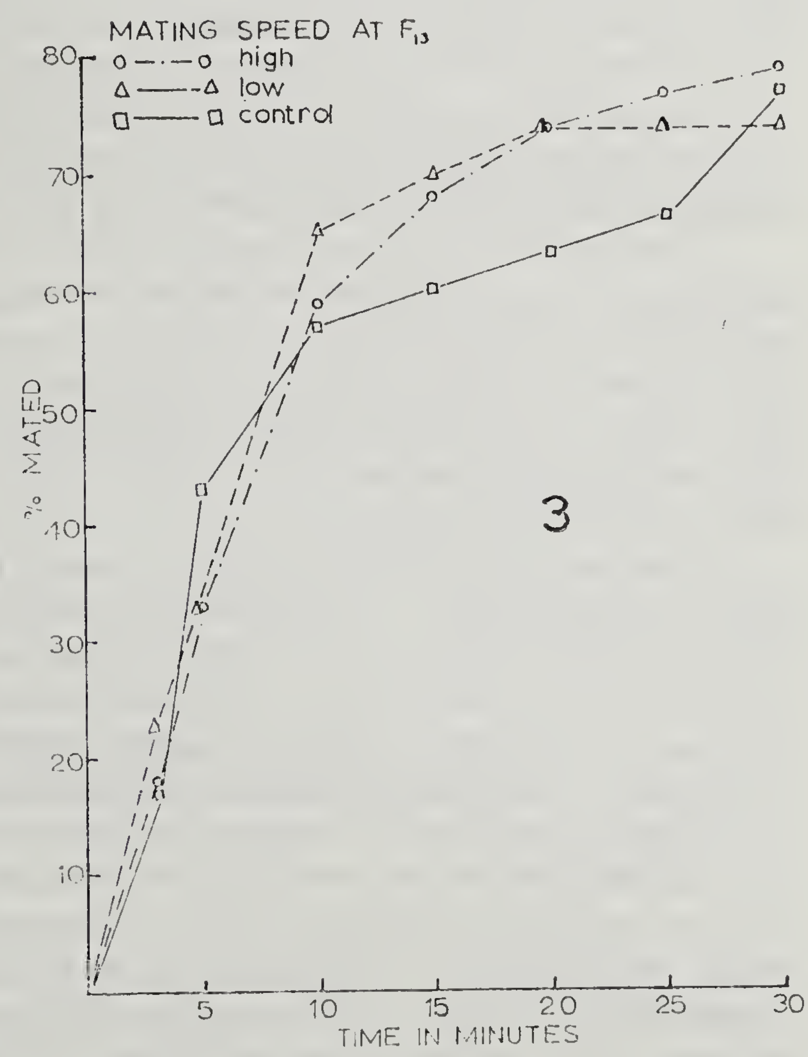
Fig. 1. Course of selection to F_{14}

Activity is measured in a perspex cell 10 × 10 × 0·5 cm., marked off into 1 cm. squares. Each fly is introduced into the chamber by tapping through a funnel, allowed 1·5 mins. to recover from this procedure, and then observed for one minute. An activity score is obtained by counting the number of squares each animal crosses during the observation period. 100 males and 100 females of the parent generation were tested, the highest and lowest scoring 10 being used to breed the F_1 generations. On subsequent tests 100 flies of each sex and each line were measured. This 10 × 10 mating design thus gives a fairly high selection pressure of 10%.

Results. The course of selection to F_{14} is shown in Fig. 1. The "low" line shows a consistent response to selection over 14 generations, correspondingly the high line after an initial rise remains fairly constant until F_{10} when a sizeable response develops over the following 4 generations. An examination of the selection curves for males and females when plotted separately shows that both sexes respond to selection to about the same extent. The unselected control line remains fairly stable about the 30 mark. At F_{14}, 20 flies of each sex and each line were tested individually in a different type of apparatus. This consisted in a series of channels, 39 cms. long by 0·2 cms. deep and 0·5 cms. wide cut in white perspex and provided with a transparent lid. This was originally designed to measure the time taken for the various groups to travel from end to end, however this proved to be impossible because of frequent turning in the tracks. Instead the distances travelled by each animal between changes in direction were measured in cm. units during a one min. test period. The results provide a confirmation of those obtained using the open field test and show that the changes in activity level are not a function of a particular apparatus.

Effects on Other Aspects of Behaviour. Manning (3) selected *Drosophila* for fast and slow mating speed, after some 25 generations of selection lines widely separated for this character were produced. He also reported significant differences in activity level between the two lines. The fast mating line was low whilst the reverse was true of the slow mating line, activity being measured in an open field apparatus. Manning concluded that the changes in mating speed were a function both of changes in threshold for sexual behaviour and also of changes in activity level, active flies responding to certain stimuli by increased activity whereas inactive





FIGS. 2-3. Results of tests at F_{12} and F_{13}

ones more quickly changed their response to one of sexual behaviour. Mating speed was measured in the high, low and control lines according to the technique described by Manning. 50 pairs of virgin flies are mass mated in a ½ pint milk bottle, as soon as they copulate they are sucked out using a modified pipette, and the time noted. The results of tests at F_{12} and F_{13} are shown in fig. 2 and fig. 3 respectively. As can be seen from these two sets of data there are no significant differences, in either rate of mating or the final point reached after 30 mins., between the three lines. Differences in spontaneous activity produced by selection have apparently no effects on speed of mating, at least, at the stage in selection so far reached. This may lead to querying Manning's argument that differences in activity level are just as important as direct changes in sexual behaviour. Doing the experiment the other way round as it were, suggests that the changes in sexual behaviour are of greater importance.

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MATING COMPETITIVENESS IN *AEDES AEGYPTI*

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Many populations of *Aedes aegypti* carry a balanced polymorphism for larval color. Larvae are either dark gray (wild type) or pale yellow, which is an albinistic form controlled by a recessive gene, yellow larva, on linkage group 2. Among different populations the proportion of yellow varies from 0 to 100%.

Experimental populations with different proportions of yellow and wild type individuals were bred continuously for more than two years. No matter what the initial composition, each population reached an equilibrium point of 70-75% yellow which is surprising because earlier work had demonstrated that yellow was usually disadvantageous.

A study to determine the factors responsible for this balanced polymorphism showed that selective advantage, heterotic effects and differential mutation all contribute to the success of yellow and that differential mating competitiveness was particularly important.

Two lines were derived from the TEXAS strain by inbreeding; one was homozygous for wild type (+ +), the other for yellow larva (*yy*). Males of these lines were compared with respect to mating efficiency. The larval color of the offspring indicated mating success. If the F_1 was all yellow, only the yellow male accomplished successful insemination. All wild type in the F_1 indicated mating by the wild type male and progeny of both genotypes indicated that multiple fertilisation had occurred. All matings were done under continuous light at 80 ± 1°F and 80%R.H.

There were 40 crosses made with a male of each phenotype kept together in the same cage with a yellow female. 65% gave only yellow offspring, 15% only wild type and 20% were mixed. In 71 crosses, yellow males were given first opportunity to mate and then were replaced by wild type males. In this situation, 93% gave only yellow progeny, 3% only wild type and 4% mixed. In the reciprocal situation (wild type first, then yellow), 69 crosses were made. These gave 56% all yellow, 22% all dark and 22% mixed.

Similar experiments were used to determine the effect of age on competitiveness. There was no difference between males 1½ days old and 4½ days old. In both cases, yellow individuals were more efficient than wild type. To assess the effects of blood feeding, crosses were made before and after the females had received a blood meal. The superiority of yellow was evident in either case. However, mixed progeny (indicating multiple fertilisation) were more frequent when mating occurred before feeding. Perhaps this is due to reduced flight of engorged females.

Does the female have a choice in mating? Males of both genotypes were allowed to compete for wild type females (+ +). F_1s were testcrossed to yellow. Phenotype of progeny indicated the type of insemination in the parental cross. The results were similar to those from experiments on competition for a yellow female; yellow males were superior. The same results were obtained with heterozygous (+*y*) females.

In summary, genes affect mating competitiveness in *Aedes aegypti*. Yellow males are more efficient in mating than wild type. They mate more rapidly and probably are more likely to fill the spermathecae. The results show that multiple fertilisation is of fairly common occurrence, although the frequency is somewhat reduced in blood-fed females. Finally, activity of the male is the index of mating efficiency, the female having little choice of partners.

HYBRIDS BETWEEN TYPICAL *PIERIS BRASSICAE* L. AND RACE *CHEIRANTHI* HÜEB

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Pieris brassicae with a widespread Palaearctic distribution is a noted migrant. Nevertheless there are a number of marked racial forms, apparently non-migrant. One of these is race *cheiranthi* in the Canary Islands, distinguishable by its larger size, the anastomising of the black markings, and pure yellowish colouration of the hindwing underside. The larva in nature feeds only on *Tropaeolum*, typical *brassicae* being mainly *Cruciferae* feeders.

A stock of typical *brassicae* has been continuously bred in Cambridge for fourteen years. Fresh adults of this stock, placed into a 25 cubic foot cage, mate several times; lay about 750 ova per female; feed on honey contained in artificial flowers.

In 1962 three *cheiranthi* were obtained and 450 ova laid. Due to heavy larval mortality only nine butterflies were reared, one pair only was obtained, resulting in twenty butterflies, which failed to mate. Apart from a few, these butterflies would not come and feed on the artificial flowers and had to be given natural flowers, or hand fed.

A male *cheiranthi* having paired with a female *cheiranthi*, was paired with a typical Cambridge stock *brassicae* and these produced F1 hybrids, which, when placed in a cage, fed, mated and oviposited freely to produce thousands of fertile F2 ova.

One of these F1 hybrids was backcrossed to *cheiranthi* and, selecting the darkest individuals, this strain was taken to the F5. In the first backcross generation nearly half the individuals died off within a few days, after which no trouble was experienced in feeding or pairing.

In 1963 a fresh stock of *cheiranthi* was obtained. In the first three generations a number of pairs were obtained but with nothing like the facility of the Cambridge stock and with very low egg production. By the F8 only one pair was obtained from several hundred butterflies. No trouble was ever experienced in obtaining hybrid pairings, and continuing these for several generations. The reason for this failure of *cheiranthi* to pair in captivity is unknown, but the readiness of typical *brassicae* to pair does appear to be inherited in the hybrids as a dominant.

The F1 hybrids are fairly uniform in larval, pupal and adult stages, being intermediate in appearance between the two parents. The F2 hybrids produce a complete range in insects between typical and *cheiranthi*, except that the *cheiranthi* type insects are absent when there is a high larval mortality.

When the backcross is performed the offspring give a range of insects intermediate between the respective parents. There are, however, various side-effects produced, in particular there tends to be an elongation of the discal spots and a tendency for ab. *biligata* forms to be produced.

These results show that the extent of the black markings, as well as other differences, are multifactorial and that *cheiranthi* is merely an isolated form of *brassicae*. In this respect *brassicae* differs from *P. napi* and semispecies *bryoniae*, where the differences are controlled by three alleles, two being dominant. Unlike *napi/bryoniae* hybrids all *brassicae/cheiranthi* broods, down to the F5 are completely fertile.

ASPECTS OF MOSQUITO GENETICS

DIMORPHISM OF MOSQUITOES

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Dimorphism is a progressively divergent feature of metamorphosis of mosquitoes. Embryos and young larvae of any one species are morphologically similar, but older larvae, pupae and particularly the adults are of two morphologic groups recognisable as males and females. As morphogenesis progresses, imaginal organs become differentiated from primordial tissues at different times. The degree of dimorphic expression of each tissue may be influenced by environment such as foreign bodies, chemicals and temperature. This is a discussion of the effect of temperature on progressive emphasis and atrophy of the imaginal organs and parts.

The distinctive features of maleness of some mosquitoes may be modified even to the point of obliteration by exposure of developing larvae to minutely controlled thermal pressure. A larva destined by its genetics to become a female does so at all survival temperatures. One bearing genetics for maleness may fulfil its destiny at normal temperatures but, in the case of some species, may be induced to become a female in whole or in part by the influence of the thermal environment. This discussion applies to *Aedes stimulans* (Walker), a species that develops in nature at a time during the spring and in latitudes where larval sites remain at temperatures below 20°C. The masculine component of *Aedes communis* may be feminised at temperatures much lower than that required for *Aedes stimulans*.

Aedes stimulans may be feminised by rearing larvae from hatching to pupation at 28·4°. Parts wholly feminised are antennae, mouth parts, claws, genital tract, gonads, and genital section of the abdomen. Scale-like remnants of the basistyles persist on the ninth abdominal segment, also. *Aedes communis* can be wholly feminised externally.

At 23·1° all parts become wholly masculine in the male genotype. Rearing at temperatures getween 23·1 and 28·4° causes progressively more extensive changes toward the feminine state. The gonads are affected at 25°; the genital tract begins to be changed and genitalia begin to atrophy at 26°; cerci appear at 27° (3).

Alternating temperatures of 23·1 and 28·4° were used to indicate the time during larval life when differentiation of a part takes place. The last two instars were most critical, and the first two influence the degree of change. Certain parts are changed when the third instar is treated, and other parts were modified when the fourth instar was under pressure. Only the gonads began to be modified when the first two instars were treated. Antennae were affected near the apex when instar 3 was under pressure. When the first three instars were under pressure and instar 4 was not, abnormal rotation of genitalia occurred and antennae were feminised. The genital tract was somewhat changed. Treatment of instar 4 caused changes in mouth parts, vasa efferentia and gonads as well as failure in rotation of the genital section. Treatment of both instars 3 and 4 caused extensive demasculinisation. Thermal pressure on the early instars conditioned the tissues for more profound changes in later instars (4).

Maximum thermal pressure when applied to the third instar in combination with the first three instars caused genital appendages to appear on the eighth abdominal segment (3). Their generation on this segment suggests that a pair of imaginal disks for appendages is present. If such is the case, these disks would seem to have persisted throughout evolutionary history from a primitive wingless state, for neopterous insects have no masculine genital appendages on the eighth segment. Genital appendages do occur on the eighth segment of female orthopteroids.

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GENETIC CONTROL OF THERMALLY-INDUCED SEX REVERSAL IN *AEDES AEGYPTI*

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Sexual dimorphism in aedine mosquitoes is conspicuous. Even in gynandromorphs, there is a clear line of demarcation between male and female tissue. However, Horsfall and Anderson (1) reported that in 12 species of subarctic *Aedes*, males may be feminised into intersexes by rearing larvae at higher temperatures. In a strain resulting from a cross between *Aedes aegypti* and *A. mascarensis*, McClelland (3) found that some of the males showed a similar phenomenon. Expression of intersexuality occurred at temperatures of 25-27°C. We find that intersexes occur regularly as 1-2% of the progeny when the F_1 of *A. aegypti-mascarensis* is backcrossed to *A. aegypti*.

We have recently discovered a different intersex-producing strain with a higher temperature threshold, in a strain of *A. aegypti* from Ganda, Kenya, that had been inbred by single-pair brother-sister mating for 17 generations. Larvae reared at 27° or 28°C gave normal adults in a 1:1 sex ratio. When larvae were reared at 30°-34°C, half the adults were normal females but the other half were intersexes. In these latter individuals, all of the dimorphic parts appeared intermediate between male and female. Larvae reared at 35°-37°C gave adults which were morphologically female. Crosses with sex-linked marker genes demonstrated that half of these "females" were genetic males.

Behavior of converted males (phenotypic females) resembled that of normal females with respect to mating and insemination. Sperm were found in the spermathecae. Blood feeding occurred and ovarian development to stage 5 of Christophers has been observed. To date, no eggs have been obtained, primarily because most of the blood meal is defecated within 24 hours. From the standpoint of sex determination, offspring from these individuals should be interesting. If Mm = ♂ and mm = ♀, the cross would be Mm × Mm and the progeny would be MM:2 Mm:mm. The phenotype of MM is unknown.

The critical period for sex conversion by heat treatment was during days 2-4 after hatching (second and third instars). Larvae treated only as first or fourth instars were unaffected. Larvae treated only in the second instar produced adult males with a second set of genital appendages growing from abdominal sternite VIII. Individuals with two sets of genitalia were fully fertile and were useful in crossing experiments. Intersexes were sterile.

Crossing experiments demonstrated that a single gene controls this phenomenon. This gene, here designated intersex (*ix*), is recessive, autosomal and sex-limited in expression. Laven (2) described a similar gene in *Culex pipiens*, although no temperature effect was involved. In both *Culex* and *Aedes*, homozygous males are feminised and females are unaffected. Among various *Drosophila* species, at least 7 intersex genes are known, but all push the female toward maleness and have no effect on the male.

The intersex gene is in linkage group 2, about 19 units from yellow larva (*y*) and 24 units from spot abdomen (*s*). The arrangement is *s-y-ix*. The values given are for a heterozygous female; crossover rate in the male is about 25% higher. It seems probable that *ix* is only a few units from the loci for resistance to DDT and dieldrin. No other morphological markers are known in this area.

In conclusion, *ix* is probably a rare gene and was accidentally discovered. The deleterious nature of a heat-sensitive gene conferring sterility on a tropical mosquito is obvious. One might speculate that the subarctic *Aedes* described by Horsfall and Anderson (1) are homozygous for a gene much like the one described here.

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MOSQUITO GENETICS IN RELATION TO THE TRANSMISSION OF FILARIAL PARASITES

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The susceptibility of *Aedes aegypti* to infection with subperiodic *Brugia malayi* is controlled by a sex-linked recessive gene (1). In male mosquitoes the distance between the gene and the sex locus, first estimated as 7-8 crossover units (2), is 3-4 crossover units (unpublished). Experiments were made to determine whether infection of the mosquito by other species of *Brugia*, *Wuchereria* and *Dirofilaria* was controlled by the same gene.

Two parent strains of *Ae. aegypti*, one susceptible, the other refractory to sub-periodic *B. malayi*, and the two hybrid F_2 generations, from reciprocal crosses of the parents, were tested against the following parasites: sub-periodic *B. malayi*, periodic *B. malayi*, *B. pahangi*, *W. bancrofti* (Malayan), *W. bancrofti* (Fijian) and *D. immitis* (Malayan). The parent strains were also tested against *D. repens* (Indian).

The pattern of infection of the mosquitoes was similar with the *Brugia* and *Wuchereria* strains; in *Ae. aegypti*, therefore, the same gene, or a closely situated one, controls susceptibility to each infection. The results with *Dirofilaria* were different. Both the parent strains and the F_2 hybrids (tested only against *D. immitis*) were very susceptible to infection; if the susceptibility of *Ae. aegypti* to *Dirofilaria* is genetically controlled, the gene or genes involved are different. The sites of development of the parasites in the mosquitoes are different, *Brugia* and *Wuchereria* developing in the flight muscles, *Dirofilaria* in the Malpighian tubules.

Four hybrid populations of *Ae. aegypti* were constituted from two parent strains, one of which was susceptible to infection with *Brugia*, the other of which was refractory. In each hybrid population the frequency of the gene controlling susceptibility was either high or low. Two populations, one with a high gene frequency (No. 1), the other with a lower frequency (No. 2), were fed for 14 generations on cats infected with sub-periodic *B. malayi;* the remaining two populations, one with a high and one with a low frequency (Nos. 3 and 4 respectively) were fed on uninfected cats. Thus the populations were controls to one another. The Table summarises the results.

Comparison of populations No. 1 and 2 and No. 3 and 4 indicates that the feeding regimen has little effect on the equilibrium frequency and that the differences between Nos. 1 and 3 on the one hand and Nos. 2 and 4 on the other are due to differences in the genetic background of the original parent strains.

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Table showing the phenotypes of four laboratory populations of *Aedes aegypti*, scored for susceptibility to infection with *Brugia*. Populations No. 1 and 2 were fed on a cat infected with sub-periodic *B. malayi*; populations No. 3 and 4 were fed on an uninfected cat.

		F_1	F_2	F_3	F_4	F_5	F_6	F_7	F_8	F_9	F_{10}	F_{11}	F_{12}	F_{13}	F_{14}
Population No. 1	Susceptible	18	11	40	43	30	18	31	32	49	19	30	59	65	51
	Refractory	13	7	23	34	53	37	50	42	59	24	64	99	80	52
	% Susceptible	58·1	61·1	63·5	55·8	36·2	32·7	38·2	43·2	45·4	44·2	31·9	37·4	44·8	49·5
Population No. 2	Susceptible	6	8	19	8	18	17	17	3	11	1	12	23	16	11
	Refractory	17	32	54	31	43	59	60	36	92	20	94	132	123	90
	% Susceptible	26·1	20·0	26·0	20·5	29·5	22·4	22·1	7·7	10·7	5·0	11·3	14·8	11·5	10·9
Population No. 3	Susceptible	22	17	28	16	30	13	26	15	19	27	23	28	26	29
	Refractory	21	21	39	26	60	44	86	51	65	82	100	133	104	76
	% Susceptible	51·2	44·7	41·8	38·1	33·3	22·8	23·2	22·7	22·6	24·8	18·7	17·4	20·0	27·9
Population No. 4	Susceptible	5	6	4	8	1	1	9	9	10	10	6	8	13	6
	Refractory	36	45	73	57	81	49	68	76	68	103	122	121	146	139
	% Susceptible	12·2	11·8	5·2	12·3	1·2	2·0	11·7	10·6	12·8	8·9	4·7	6·2	8·2	4·1

GENETIC DISTORTION OF SEX RATIOS IN *AEDES AEGYPTI*

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Craig, Hickey and VandeHey (1960) reported that a hereditary factor was responsible for high male ratios in *Aedes aegypti.* They found that male-producing (*MP*) is transmitted only by males and is not due to differential mortality, at least in postgametic stages. Hickey and Craig (1962) presented preliminary data on the inheritance of *MP* and hypothesised that a "drive mechanism" was involved.

The purpose of this paper is (1) to present genetic and cytological evidence explaining how *MP* operates, and (2) to describe the behaviour of *MP* in experimental populations.

MP can be carried in certain strains without expression, showing its effect only on outcross. Matings within strains homozygous for this factor (+ +) produce sex ratios of about 1 : 1. A second type of strain lacks the *MP* factor (– –) and matings within these strains also produce sex ratios of about 1 : 1. The following diagram shows the results of reciprocal crosses between *MP*-positive and negative strains (Mm = ♂, mm = ♀):

P:	$m^-m^- \times M^+m^+$	P:	$m^+m^+ \times M^-m^-$
F_1:	M^+m^-(1:1 sex ratio)	F_1:	M^-m^+ (1:1 sex ratio)
F_2:	distorted sex ratio	F_2:	1:1 sex ratio

MP functions only in the male and is operational only in the heterozygous condition (+ –). Moreover, the + must be on the male-determining (M) chromosome. These results are in accordance with models of meiotic drive in *Drosophila*.

Do *MP* males produce as many functional sperm as normal males? Ejaculatory glands of *MP* and normal males at different ages were compared. *MP* males depleted their sperm supply more rapidly than did normal males. Perhaps female-determining sperm never reach the ejaculatory gland.

Experimental populations were established to follow the effect of *MP* over a series of generations. In the first set of experiments the generation time was distinct. The parental generation consisted of m^-m^- females and M^+m^- males. The sex ratio was recorded for 14 filial generations. Sex ratios were distorted for the entire period, although the effect of *MP* was reduced in later generations. In the latter, test crosses demonstrated that *MP* was still present even though the sex ratio approached 1 : 1. The expression of *MP* was probably masked by systems of genetic modifiers which gradually rendered the (m^-) chromosomes insensitive. An insensitive strain was transformed into a sensitive one by inbreeding without selection, probably through the elimination of modifying genes.

In a second set of experiments, populations were maintained continuously without separation of generations. Again females of a sensitive strain were exposed to *MP* males. Distortion of sex ratios (about 20% ♀♀) continued for more than 25 weeks. When *MP* males were introduced into an insensitive population (m^+m^+), an initial distortion of sex ratio occurred, followed by a rapid return to normal. In the control cage containing only normal males and females, the sex ratio remains normal.

MICROEVOLUTION

EVOLUTION OF COMPLEX POLYMORPHISM AND MIMICRY IN DISTASTEFUL SOUTH AMERICAN BUTTERFLIES

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The genetics of polymorphism in Batesian mimicry is well understood (5); that of Müllerian mimicry is not, and indeed genetical theory predicts that warningly coloured and distasteful species should be monomorphic. The rampant mimetic polymorphism of many *Heliconius* is therefore highly interesting, as the butterflies are distasteful (experiments with caged birds (1)), warningly coloured, and attacked by birds in the wild (beak-marked specimens). *Heliconius* species mimic Danaids, Ithomiids, Acraeids and other Heliconiidae; there is evidence that some instances of intrageneric mimicry involve convergence of pattern rather than retention of common ancestral patterns. The two most variable species, *H. melpomene* and *H. erato*, have about thirty morphs each, and are mutually mimetic, almost every morph of one being paralleled by a similar and usually sympatric morph of the other; some patterns are shared by about ten *Heliconius* species. Factors other than mimicry must affect the polymorphism, as some pairs of morphs are allopatric, and some morphs are non-mimetic, notably the widespread green form of *H. doris*.

The polymorphism of *melpomene* and *erato* in Guiana is controlled by several loci, unlinked, loosely linked, and very closely linked as a supergene (7, 9). Both the known selective forces—sexual selection, which favours increase of red (3), and visual predation, which favours the commonest form, even if we apply models of epistatic selection acting on linked genes (4)—should eliminate the polymorphism. Because extensive monomorphic populations alternate with polymorphic, because peripheral populations are monomorphic and because the morphs in polymorphic zones are those we would obtain by hybridising the monomorphic populations on either side, it is likely that much of the polymorphism results from the hybridisation of subspecies once isolated by climatic cycles in the Pleistocene (c.f. *Papilio dardanus* in Africa (6, 8) and Lycaenids in the Antilles (2)). Even here complex factors must have acted after hybridisation, as in Guiana we should find forms with black-based forewings and rays on the hindwings, but these are completely absent, and while some of the *melpomene* with narrow red bands on the forewings are heterozygotes for the gene producing a broad red band and that producing a group of yellow spots (7), some narrow bands are produced by a different recessive gene (9), probably not found in either "parent" population. In *H. doris*, di- or trimorphic through most of its range, the polymorphism shows no sign of resulting from hybridity.

Elucidation of the *Heliconius* problem should greatly increase our understanding of the evolution of polymorphism and of colour patterns. A detailed study is in preparation.

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EXPERIMENTAL STUDIES ON MICROEVOLUTION IN POPULATIONS OF THE LEPIDOPTERA

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The pioneer field work of Dobzhansky, Fisher, Ford, Timofeeff-Ressovsky, and others in the 1940s revealed that natural selection is often more intense than was assumed either by Darwin or by the earlier population geneticists. However, even now we have comparatively little data on the actual change in selective value for any given change in a character in any particular population in nature. Consequently, we have little idea of how small the change in a character has to be before its evolutionary consequences are unimportant even in quite large populations. The paper describes three investigations designed to estimate selective values in nature and to detect the evolutionary consequences of small changes in phenotype.

1. In the warningly coloured Scarlet Tiger Moth, *Panaxia dominula*, there are two forms, *medionigra* and *bimacula*, which are respectively heterozygous and homozygous for a gene only known to be common (about 2%) in one natural population. New colonies have been founded with gene frequencies of the order of 25% and 50%. The gradual reduction in the frequency of this gene in the colonies has been studied in order to measure the selective intensities operating.

2. The pale (typical) and melanic (*carbonaria*) forms of the Peppered Moth, *Biston betularia* have been used in order to try and determine the selective advantage of the melanic over the typical form in industrial regions. From a study of the disappearance of dead moths off tree trunks, the expectation of life of the melanics in the wild and the frequency of the melanics in populations near Liverpool, it is concluded that the selective advantage of the melanics may be of the order of 30%-50%, a value which agrees well with that obtained from Kettlewell's 1955 experiments. The data also suggest that the homozygous melanic is at a disadvantage of about 5%-6% to the heterozygote (Clarke and Sheppard, unpublished).

3. Genetic and morphological studies of the mimetic butterflies *Papilio dardanus* and *Papilio polytes* suggest that very small changes in the lengths of the "tails" on the hind wings can have important evolutionary consequences (Clarke and Sheppard, 1963, unpublished). Moreover, theoretical considerations and experiments (3) suggest that very small changes in the phenotype will be appreciated by a potential predator and are, therefore, not neutral in survival value.

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CHROMOSOME INVERSIONS AS BLOCKS TO GENETIC EXCHANGE LEADING TO SYMPATRIC SPECIATION IN BLACK FLIES (SIMULIIDAE; DIPTERA)

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The integrity of any species depends (*a*) on mutations being spread throughout a population by "gene flow" and (*b*) by "genetic recombination" at meiosis. Speciation results from failure of either or both these processes. Allopatric speciation results from the blocking of gene flow between populations of individuals isolated by barriers or isolating mechanisms (5). Sympatric speciation presents a puzzling paradox because gene flow operates at all times throughout the species. Chromosome inversions, already established as crossover suppressors, for the same reasons, function as blocks to genetic exchange (6), by creating within a species alternate yet isolated populations of chromosome segments (standard, "s"; inverted, "i")

between which "gene flow" is blocked. These two alternates could eventually accumulate enough mutations to effect speciation sympatrically. The principle end result which could be observed in the giant chromosome of two new sympatric sibling species would be banding patterns that differed by a single inverted region (3). This process can be represented schematically by $ss \rightarrow si - \begin{cases} \rightarrow ss \\ \rightarrow ii \end{cases}$, the heterozygote, si, eventually disappearing from natural populations. Situations like these are the rule rather than the exception in Simuliidae (1-4).

Figure 1, one of several similar charts showing phylogeny within species groups in Simuliidae (1-4 and unpublished data), shows the nine known cytological segregates (A to J) and one ancestral hypothetical (Hy) of the *aureum* group in *Eusimulium* (3). The chart was derived by tracing the observed inversion differences between species (number of steps shown between letters). Without further evidence there is no way of telling phylogenetic direction since phylogeny can be traced readily from any point in Figure 1. However in certain cases where two inversions are involved together, development from the intermediate step ($ss + ss \rightarrow si + si$) could be in one of two ways: (*a*) $si + si - \begin{cases} \rightarrow ss + ss \\ \rightarrow ii + ii \end{cases}$, a cis-type disjunction or (*b*) $si + si - \begin{cases} \rightarrow ss + ii \\ \rightarrow ii + ss \end{cases}$, a trans-type disjunction in which the chromosomal progenitor evolves out of existence. Where a trans-type disjunction is suspected and the lost arrangement of the progenitor can be determined, the observed results can only be obtained in one way, thus establishing phylogenetic direction.

Figure 2 was developed by (*a*) assuming sympatric speciation based on inversions wherever possible and (*b*) deducing phylogenetic direction from the trans-type disjunction that led to the development of A and B from Hy. Since form G has preserved the two critical "floating" inversions of Hy (3) and because Hy and C share the same banding pattern, form C is definitely established as the progenitor of A, B and G. For various reasons to be published in detail at a later date, form E (*E. aureum* Fries) is assumed the progenitor of C and D, and as a matter of convenience, of F, I and J as well. Because allopatric speciation allows species to have identical banding patterns Hy and C developed allopatrically probably to the west and south of a North American Pleistocene ice sheet.

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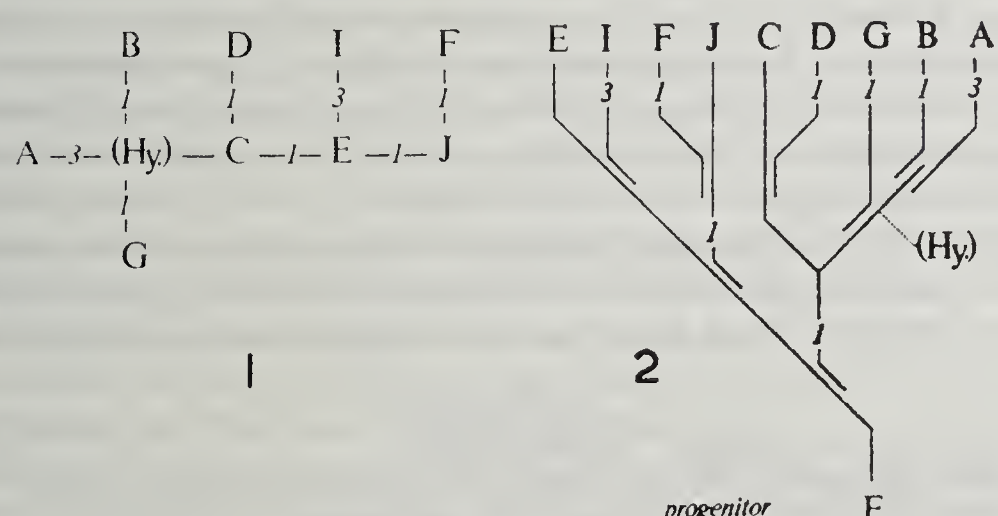

Figs 1-2. (1) Phylogenetic relationships: species found sympatrically—Nearctic A B D, C **D**, B G—Palaearctic B E F J, E F I. (2) Phylogenetic descent: open disjunction shows sympatric speciation, closed disjunction shows allopatric speciation.

THE PROBLEM OF THE *ANOPHELES GAMBIAE* COMPLEX (DIPTERA)

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At least 5 mating-types constitute the *Anopheles gambiae* complex as it is known to-day:

A. melas Theobald, a salt-water tolerant form confined to the west coast of Africa.

A. merus Dönitz, a salt-water tolerant form confined to the East Coast of Africa and islands off it.

A. gambiae A } { fresh-water forms occurring over the whole continent, often together in
A. gambiae B } { the same locality (4).

A. gambiae C, an almost exclusively exophilic and zoophilic fresh-water form so far only recorded in Southern Rhodesia and Swaziland (2 and 7).

Crossing any two of these five forms results in sterility in the hybrid male. In addition, crossing A or B males with *melas*, *merus* or C females results in a marked excess of males in the F_1 generation. The F_1 female (at least in crosses between A, B, *melas* and *merus*) is fertile and can be backcrossed successfully.

Detailed morphological studies of *melas*, *merus* and the fresh-water forms A or B by Coluzzi (1) have revealed fairly consistent differences between *melas* and *merus* and between these two and the fresh-water forms taken together, but no real differences are apparent between A and B. C has not yet been studied in detail.

The evolutionary status of *melas*, *merus* and form C would seem to be that of full species in the strict genetical sense. Each can be found existing sympatrically with the A or B fresh-water forms and yet retaining its identity over long periods of time. In areas where *A. melas* and fresh-water *A. gambiae* co-exist, for example, separate peaks in density are usually apparent, the one dependent on tides and salinity (*A. melas*), and the other dependent on rainfall only (*A. gambiae*), (Giglioli, personal communication). A remarkable example of the separate existence and the differing vectorial capacities of *A. merus* and fresh-water *A. gambiae* has been recently given by events on the island of Pemba following house-spraying with the insecticide dieldrin (5). Virtually no fresh-water *A. gambiae* were to be found for a long time after this spraying, though plenty of *A. merus* were in evidence both as larvae and as outside-resting adults. The malaria incidence had at the same time fallen to a very low level. An equally remarkable state of affairs is to be found in the Mazoë Valley, Southern Rhodesia, where all three forms of fresh-water *A. gambiae* are known to co-exist. The prolonged use of BHC in houses in this area has resulted in the replacement of a population predominantly A and B, which are endophilic, anthropophilic malaria vectors, by a population predominantly C, which is an exophilic, zoophilic, non-vector. This apparent behaviour change as the result of the prolonged use of an insecticide is in fact interspecific.

The exact status of fresh-water forms A and B remains to be finally determined. The sympatric existence of these two forms is known from several localities and mixed colonies have been raised in the laboratory from eggs sent from the field. No sterile males have been found in such colonies. However, crossings between the two forms from different localities have proved easy in the laboratory and field evidence exists of the natural occurrence of sterile males in significant numbers (Coz, personal communication). No evidence yet exists of differing malaria vectorial capacity between the two forms and dieldrin-resistance is present in both in West Africa and in neither in East Africa. Paterson (6) is certain that the two forms warrant full specific rank. Davidson (3) is more cautious and prefers to call them semi-species.

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GENETICS OF *TRIBOLIUM*

SOME REMARKS ON THE BIOLOGY OF *TRIBOLIUM*

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Five species of *Tribolium* are found fairly frequently in stored produce and all are easy to culture. Hinton placed these in two groups *castaneum* and *madens*; *confusum*, *anaphe* and *destructor*. *T. castaneum* is the most widespread and abundant especially in the tropics; *T. madens* is a rarity apparently found mainly in areas of extreme continental climate; *T. confusum* is typically an inhabitant of the milling stream of flour mills; *T. anaphe* is a recent invader of groundnuts in W. Africa and *T. destructor* a temperate species most common in Scandinavia. I have worked with the first three species and have data on the fourth supplied by Mr. E. T. Bezant. I rely entirely on the literature for numerical data on T. *destructor*. The tendency to cannabalistic habits of the two common species is well-known and it is probable that these, and fairly certain that the other three, thrive better on diets containing animal protein such as dead insects which may well have been the major constituent of their diet in their initial (pre-human) habitat.

The abundance of each species is related to its ability to multiply in laboratory experiments as can be illustrated by comparing their rates of development. Larval development is much faster in *castaneum* and *confusum* than in the other species, *castaneum* growing the faster above about 27°C and *confusum* below this temperature. Below 20°C only *destructor* apparently is able to develop satisfactorily, this species having a maximum about 32°C. The *castaneum-madens* group develop more quickly than the other group in the egg and pupal stages, so that taken over the whole life cycle *castaneum* develops faster than *confusum* down to 25°C.

All five species can be conveniently used as laboratory experimental animals because they are easily bred and complete a generation in about a month. However, there are a number of points that are worth considering. Field populations and most laboratory stocks which are not deliberately inbred are probably polymorphic for developmental rate characteristics, up to 5 per cent growing rather more slowly than the main population. The two sections of the population overlap but fortunately they can be segregated if each pupa is weighed on the day it is formed. Within each sector the weight decreases as the period of development increases, but the individuals of the group that grow more slowly are heavier than the other group. Consequently if weights are plotted against developmental period for each sex separately, the two populations can be differentiated. The separation may be done objectively using probability paper. Some half-hearted experiments with selected individuals seemed to suggest that the minor population could be eliminated when no individuals growing slowly appeared in the third generation, but in the fourth, these appeared again in larger numbers than usual.

For my purposes it is convenient and necessary to grow larvae individually. For most people this is clearly inappropriate, but the tendency in general is to work at too high a density simply because the insect tends to grow to its own saturation level. High densities have several consequences. Firstly the temperature in the experimental vessel probably rises at least 2°C above the controlled environment, possibly more, so that experiments comparing density levels will not be all at the same temperature. Weight, for instance, decreases as temperature increases and in any experiment involving food renewal there will be built-in cycles of temperature and food supply which may vary with the age composition. Overcrowding will encourage the eating of eggs and pupae. In my experience egg-eating by adults, starts accidentally but is habit forming. Similarly the eating of pupae is induced by shortage of food or space and is influenced by the spread of age of larvae.

In addition the development may be influenced by crowding. Naton found pupation of *destructor* delayed by crowding; I found pupation of *madens* delayed by temperatures in the lower part of the range suitable for development. These may be related to a need for some minimum bodyweight (or other factor related to this) before pupation is possible.

Growth rates are obviously related to food but it is perhaps less obvious that they are related to its particle size, generally the smaller the particle, the easier it is to eat them. Mould in the food may hinder physically, or be toxic, or supply some desirable constituent which is lacking.

Most of these points are probably unimportant to those students of *Tribolium* genetics who are only searching for elementary facts but must be considered as soon as the study deepens and considers "fitness" and other ecological and evolutionary fundamentals. It seems very likely that "fitness" by whatever concept it is defined will differ with wide varieties of environment. If experimental techniques induce fluctuation of population size, the selection of individuals and genes that succeed in dense conditions may lead to failure in sparse populations or the fluctuations might preserve both characteristics. Stock breeding in dense conditions at or near the optimum would if there is additional heating yield a high temperature strain, and in any event often eliminates some biological characteristics such as a facultative diapause as well as allowing some homozygous recessives to appear.

However, if we try to avoid wholesale food replacement by using a compartment method of experiment, the presence of a series of containers each with a different environment opens up a new line of ecological and behavioural research. The mention of behaviour also makes it necessary to point out that stored products insects do not always choose what is best for them so that it is not profitable to rationalise experimental results. In any event, a great deal of these results are not due to choice but can be explained by assuming random movement and changes of behaviour in different environments.

A RE-EVALUATION OF REYNOLDS' STUDY OF THE INHERITANCE OF FOOD EFFECTS IN *TRIBOLIUM DESTRUCTOR*

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Introduction. Reynolds (1) studied the effect of flours of different extraction rates when fed to larvae and the resulting adults of *Tribolium destructor*, upon the rate of development of the first filial larvae. He claimed to have found evidence that the parents' food affected the rate of development and mortality of offspring. Even though this observation can be explained on non-Lamarckian grounds, it is remarkable in itself. If such effects truly occur, this pattern of response will require modifications to be made to the generally accepted ideas on population growth. Obviously, Reynolds' results should be subjected to re-examination and, if they stand scrutiny, an attempt be made to repeat his observations.

Reynolds' statistical methods are open to criticism. He gives in his table 1 the mean and standard deviation of the post-oval development periods on 12 different food combinations and, he states, "Fisher's *t* test (*sic*) has been used to compare these results".

Methods and results. It is now impossible to examine Reynolds' original experimental records. In any case there are so many gaps in the table as not to make an analysis of variance worthwhile. However, it seems that for his conclusions to have been justified, his evidence should support the relationship $y = b_0 + b_1x_1 + b_2x_2 + b_2x_3$ where the b_i are constants, x_i the composition of the foods as in table I and y is the developmental periods of the filial generation.

The estimates of the regression coefficients and the analysis of variance associated with them are given in table I (i). It can be inferred that this regression relationship could occur frequently by chance if y was independent of the x_i. Of the regression coefficients, only one seems to be different from zero; it is that which relates the developmental period of the larvae with the food that their parents had eaten as adults. It seemed worthwhile, therefore, to study the relationship of these two factors alone, without making any allowance either for the food the parents eat as larvae or for the food of the filial larvae. This relationship is thus of the form $y = a + bx_2$ where a is a constant. The estimate of b is given in table I (ii) together with an analysis of variance; a chance relationship of this kind would occur about once in thirty times if there were no relationship between the two variables.

Discussion. Reynolds' data suggest that the developmental period of larvae of *T. destructor* is independent of their food but is determined primarily by the food of their parents as adults. This is a biological paradox; it is now inferred that the regression analysis in table I (ii) has

TABLE I

Partial regression coefficients, with their standard errors in parentheses, and an examination of them in relation to the null hypothesis

(i) $b_1 = -0{\cdot}019\ (0{\cdot}121)$; $b_2 = -0{\cdot}271\ (0{\cdot}132)$; $b_3 = 0{\cdot}104\ (0{\cdot}129)$

Analysis of variance

Source	*Degrees of freedom*	*Mean square*	*F*
Regression	3	24·8	1·6
Residual	7	15·9	

(ii) $b = -0{\cdot}280\ (0{\cdot}102)$

Analysis of variance

Source	*Degrees of freedom*	*Mean square*	*F*
Regression	1	84·3	7·5*
Residual	9	11·3	

* $P \simeq 2{\cdot}5\%$

recognised no more than a spurious relationship. It is concluded that Reynolds' inferences were unjustified on his data; if they are insufficient to establish that larval development was directly affected by the nutritional quality of their own food, how can they be taken to support other than a chance relationship between larval development and parental food?

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STUDIES OF NATURAL SELECTION IN *TRIBOLIUM CASTANEUM* HERBST (COLEOPTERA) IN TWO DIFFERENT MEDIA

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Two sets of populations are under investigation. The first set includes replicate populations started with 20 pairs of beetles heterozygous for pearl, (*p*), black (*b*), and microcephalic (*mc*), (genes located in separate linkage groups). The genes have been introduced, one at a time, two at a time and three at a time into jars containing standard medium (whole wheat flour plus brewer's yeast) and maintained in an incubator set at 32° and 70 per cent relative humidity. Thus, at introduction, each gene had a frequency $q_o = 0{\cdot}50$. Flour beetles are long lived and generations may overlap. To prevent this, artificial generations were created by scoring and discarding the adults at census time (one per month) and returning the pre-imaginal stages to their jars.

The second set includes four populations started with 20 pairs of $p/+$; $b/+$; $mc/+$ beetles in corn meal (of the same particle size as the whole wheat flour) + yeast, but otherwise treated in the same manner as the other populations.

In the first set of populations (in whole wheat flour), carried for the most part for 14 generations, the autosomal recessive *mc* which affects the size of the head (behind the gena) and of the compound eye, and which exhibited only a slight (10 per cent) reduction in viability in preliminary tests, has been eliminated rapidly (at a rate equivalent to $s = 0{\cdot}8$–$1{\cdot}0$), regardless of what other genes are present; the autosomal semidominant body color gene black declined in frequency very slowly (at a rate similar to that corresponding to $s = 0{\cdot}05$–$0{\cdot}10$); the autosomal recessive eye color gene pearl gave inconsistent results: in some populations the gene declined gradually but steadily, at a rate equivalent to that given by a theoretical curve with $s = 0{\cdot}05$. In others, the gene declined more rapidly for a few generations ($s = 0{\cdot}2$) but then the gene frequency of *p* increased, producing a curve similar to one favoring the heterozygote, with $s = 0{\cdot}1$ against the pearl homozygote and $t = 0{\cdot}3$ against the wild type homozygote. The number of adults observed in all populations was between 400 and 645 on the average, and the shift to a predominant pearl genotype appears to have occurred in some replicates when the numbers of adults in the preceding generation was low, but a low density of population is not a requirement for such a shift.

These results are at variance with those reported by Kollros (1944, unpublished Ph.D. thesis, University of Chicago) who found a decline in the gene frequency of pearl in populations allowed to overlap in generations, despite the fact that in many of the characters measured (fecundity, larval survival, cannibalism, etc.) the heterozygote was superior. These results also appear to be at variance with some results hinted at by Sokal and Karten (1964, Genetics 49: 195) who have reported a possible $\hat{q}=0{\cdot}8$ for the *b* gene in some of their populations.

Preliminary tests had shown that *T. castaneum* is less productive in corn meal + yeast than in whole wheat flour + yeast, but more productive in these two media than in corn alone. The numbers of adults observed in the populations reared in the corn + yeast medium average between 165 and 345 adults confirming the observation that this species does not do as well in corn as it does in wheat flour + yeast.

In the corn meal plus yeast medium, the fate of *mc* has been the same as in the wheat populations: at the end of seven generations the decline of the frequency of this gene fits the curve produced by a theoretical selection against the recessive $s=0{\cdot}8\text{–}1{\cdot}0$ for at least three of the populations. In the fourth population $q_7=0{\cdot}25$, which is much higher than the theoretical value expected ($q_7\simeq 0{\cdot}15$). In regard to the other two genes, the populations fall into two groups: in one (two replicates) the *b* population has declined with a slope similar to that of curves produced with $s=0{\cdot}05\text{–}0{\cdot}10$. In the other replicates *b* has increased in frequency over 50 per cent, a phenomenon which had not been observed in the wheat medium. Most noteworthy is the performance of pearl in corn: this gene showed an immediate rise in frequency over 50 per cent, in some cases reaching a frequency of about 70 per cent at the end of five generations.

Discussion of these results will be focused on the concept of adaptive value. In the data presented, it is clear that adaptive values in some populations and for some genes have changed in the whole wheat medium after several generations, and that they are of a different order of magnitude when different media are used. At the present time it is not known whether this is a result of the different nutrients, or to the fact that different densities prevail in the two media, with the result that competition between genotypes is not as intense in corn flour + yeast as it is in whole wheat flour + yeast.

COMPONENTS OF SELECTION IN *TRIBOLIUM* (COLEOPTERA) AND HOUSEFLIES [1, 2]

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Work on the ecology of natural selection has progressed using mutant strains of houseflies (*Musca domestica*) and the flour beetle *Tribolium castaneum*. Recent work on the competition of housefly larvae involving the *green* locus (*ge*) has been reported (1). With increasing density, adult weight was reduced before survival declined. Recent studies of the reproductive performance of adults reared from larval cultures of different densities indicated that housefly adults can sustain a weight reduction of up to 40% without much effect on fecundity or the innate capacity for increase.

Larval competition among genotypes involving the semidominant *black* locus (*b*) in *Tribolium* has been reported (2). Effects of density on survival, weight and length of developmental period differ with genotype and with the gene frequency of the populations. Examples of genetic facilitation were found.

These *Tribolium* experiments are related to a long term selection experiment in which the adults, after they had all emerged, were allowed to oviposit in flour for three days to produce a new generation. Then, after being counted and classified as to genotype, they were discarded. Thus *Tribolium* is made to simulate an organism having a brief adult life and non-

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overlapping generations. By artificially restricting the normally long adult life-span, the evolutionary effects of natural selection are likely to be speeded up. The experiment was done in small jars containing 40 gms of medium. There were three + + replicate populations, three *bb* and five populations each, started at the Hardy-Weinberg genotype ratios, for the gene frequencies $0{\cdot}75q_b$, $0{\cdot}50q_b$, and $0{\cdot}25q_b$.

The growth of these populations, as expressed by the changes in adult numbers, is as follows: the + + populations level off at a density around 1,200 adults, the *bb* at a slightly lower density, while the mixed cultures produced nearly double that number (1,700–1,800 adults). Although net fecundity drops rapidly with increasing density of adults, *bb* populations produce nearly twice as many eggs as + +, the mixed cultures being intermediate. Some preliminary experiments with marked eggs indicate that most of this difference may be due to a much lower rate of cannibalism of eggs in the *bb* strain. The survival of the immature stages is quite high for the + + and mixed cultures, ranging from 0·65 to 0·55 over a wide range of egg densities—up to 4,000 egsg. Mortality is due, mostly, to cannibalism of pre-moult larvae, prepupae and pupae by active larvae. The populations of *bb*, however, have poor survival (about 0·35) above densities of 2,000-2,500 eggs, which results in low populations of adults in spite of the much higher egg production. The different genetic populations differ in another character of the growth form. Fluctuations in numbers of adult + + are quite small whereas those of *bb* are quite pronounced. The mixed cultures also exhibit fairly large fluctuations in numbers, being most prominent in the $0{\cdot}75q_b$ cultures and least in the $0{\cdot}25q_b$ cultures.

During the first fifteen generations, the gene frequency of *b* in the populations started at $0{\cdot}25q_b$ rose to about $0{\cdot}55q_b$; that in the $0{\cdot}50q_b$ populations rose to $0{\cdot}65q_b$ and the $0{\cdot}75q_b$ populations, after an initial drop, returned to $0{\cdot}75q_b$. At the present time little change is occurring. During the first eight generations we maintained duplicate jars produced during a second three day period by the adults of each experimental jar. At appropriate times, samples of eggs, small and large larvae, and pupae were removed and reared at low densities until their phenotypes could be distinguished. In this manner, the life stage at which any selective forces acted could be more closely determined. Nearly all the duplicate jars exhibited, to various degrees, the following pattern: (*a*) a shift toward increased frequency of *b* occurring in the egg stage, (*b*) a reverse shift in the larvae, and (*c*) a shift, sometimes marked, toward an increase of *b* from pupa to adult. Little has been done as yet to investigate the oviposition rates of the different genotypes, but there is some evidence that among young adults, *bb* individuals have a slightly higher oviposition rate. The shifts in the larvae and pupae can be explained by assuming that + + individuals have a faster developmental rate. There would then be an increased cannibalism of smaller pre-moult +*b* and *bb* larvae. The early pupating + + individuals would, however, fall victim to the slower +*b* and *bb* large larvae. Individuals pupating later would suffer less mortality from cannibalism because there would be fewer larvae present. Although there would be more adults at this later time, they are much less cannibalistic than are the larvae.

In a duplicate jar where the gene frequency was $0{\cdot}58q_b$ and the initial egg density was about 3,000 eggs, pupae were removed every day as they formed. There were proportionally more + + pupae occurring during the first few days of pupation than later. In this instance, pupation occurred over a period of 41 days. If most of the pupae from the first 19 days were cannibalised (which is quite likely if they had not been removed from the jar), the gene frequency of *b* among the survivors would have been altered from $0{\cdot}58q_b$ to $0{\cdot}60q_b$. This is, in fact, what occurred in the corresponding jar in the selection experiment. Repetition of this experiment with other duplicate jars confirms these results. Comparison of the number of adults produced in these jars with the numbers produced in similar jars where the pupae are left undisturbed provides some estimate of the mortality due to cannibalism of pupae. Thus, it is probably cannibalism of the faster developing + + prepupae and pupae that was responsible for the increase in the frequency of the *b* gene in the $0{\cdot}50q_b$ and $0{\cdot}25q_b$ populations. What the complex of factors is that halts this process and brings about an equilibrium condition is still not clear.

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COMPARATIVE GENETICS OF DIPTERA

THE GENETICS OF THE HOUSEFLY

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The study of the basic genetics of the housefly was started some twelve years ago in order to reach a better understanding of its biology, mainly in relation to insecticide resistance.

Genetical studies started with a search for mutants, by inbreeding normal flies from field populations which could be described as *domestica* s.s. or as *vicina* Macquart (6). Exactly similar results have been reached in different laboratories (4, 14 and 16).

A host of minor mutants, mainly affecting wing venation or chaetotaxis, can be recovered from any field population or laboratory colony; their phenotypic properties are usually poor, but can be improved by selection.

Mutants giving similar effects, due to different genes, are common; e.g. the eye color mutants, three causing yellow eyes (*ocra*, *green eyes*, and *yellow eyed*), one causing white and two causing pinkish eyes; one, *carmine*, is linked with the locus *a*, controlling aliesterase activity (2); all the mutant eye colors change with ageing, although to different degrees.

Homeotic mutants are common; *aristapedia* turns the arista into three tarsal segments; the main bristles are thinner than normal; it has good phenotype properties and is a good marker for the chromosome carrying the *aliesterase* gene; *antennapedia* affects the antennae, which are turned into legs, with varying expressivity; it does not breed true, and behaves either as dominant or recessive according to the strains in the cross; *abdominal legs* causes the appearance of legs on the abdominal segments of about one-third of the flies; it disappears after crosses.

An example of epistasis is given by *spindle* which reduces the eyes to narrow vertical spindle-like structures; in homozygous *spindle* flies, *ocra* can be seen only when the expression of *spindle* is very poor; *spindle* is recurrent in related strains, but complex phenotypes are common. As an example, the mutant *runt* reduces the body size, affecting also length and shape of wings, legs and bristles which are irregularly placed; when *runt* coexists with *aristapedia*, the tarsal segments replacing the arista can be greatly shortened, providing an obvious example of factorial interaction.

Coexistence of distinct effects is by no means rare (7). The character *tf* (fused tarsal segments), conspicuously affects wings and legs; it tends to become less pathological if selection for high expressivity is not applied; wings and legs are controlled by distinct sets of modifiers; it behaves as a recessive pleiotropic mutant, but, when first isolated after outcrossing, it requires selection for several generations, because a minority of flies continuously reappear having normal legs: their wings are affected only by additional veinlets on the posterior crossvein.

The recessive autosomal male-limited *countercoiled* (*ctc*) reverses the coiling direction of the hypopygium and the disposition of the asymmetrical sclerites of the male terminalia; well developed terminalia of *ctc* males are a mirror-image of the normal ones.

When *ctc* first segregates after outcrossing, incomplete rotations are common and coexist with underdevelopment of the so-called "synsternite 7-8"; the degree of rotation and the development of this sclerite are closely related (13); gynandromorphs with suitable combination of sclerites indicate a tergal origin for (their) "synsternite 7-8" (7).

Incompleteness of rotation causes mechanical impediment to copulation in otherwise perfectly normal males, enforcing natural selection for full expressivity of the mutant gene and for its best integration with the residual genotype.

The mutant *brown body* (*bwb*), possibly homologous of *yellow* of drosophilas, is a very good marker of the second linkage group, which includes factors for DDT-resistance. Generally inherited as an autosomal recessive, it follows holandric inheritance when introduced in some American strains (2 and 10), as can do all the markers of the same linkage group, according to Sullivan (15) who named this condition TYII; holandric inheritance of a gene causing DDT-resistance has been described by Kerr (3).

My colleague Dr. Rubini, has recently shown that the strains differing for the mode of inheritance of the *brown-body* marker have Y-heterochromosome of different sizes and forms (8); hybrids between two such strains had the autosomes of the largest pair partly different.

Linkage data have been published (12, 10, 11, 7, 4 and 16); nomenclatorial confusion obtains as a consequence of lack of coordination between laboratories engaged in overlapping programs.

The only attempt to study population dynamics is provided by observations on the distribution of the gene *kdr* (DDT-resistance) in the province of Latina (9). A field survey has revealed that the frequency of DDT-resistant house-flies differs between districts, which had different insect control histories because of their eco-geographical properties; toxicological tests on field-samples and on their F_1 progenies have provided similar results, with the exception of samples from mountains, where the frequency of resistant flies has been higher in the F_1; a control campaign with Diazinon did not affect the relative frequency of DDT-resistant flies; genetical and toxicological tests provided similar information on the frequency of the gene *kdr,* the main cause of DDT-resistance in these populations at the time when the survey was performed.

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SECTION 5.—BEHAVIOUR (INCLUDING THAT OF SOCIAL INSECTS)

The following papers were read but their authors did not wish them to be published here:

Barth, R. H., (U.S.A.). Cockroach Mating Behaviour: Neuroendocrine control of a chemical communication system.

Brower, L. P., (U.S.A.). Exploitation of the behavioural repertoire of vertebrate predators in evolution of protective coloration.

SPATIAL ORIENTATION OF INSECTS

SUR LE ROLE DYNAMOGENIQUE DES ORGANES SENSORIELS DANS L'ORIENTATION DES INSECTES

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Les organes sensoriels des Animaux exercent une double fonction: ils délivrent des informations concernant le milieu extérieur et intérieur, ainsi que la motricité du corps propre; d'autre part, ils contribuent à maintenir le système nerveux central à un niveau suffisant de réactivité (ou de vigilance). Chez les Vertébrés, ce deuxième rôle est bien connu depuis les recherches de Moruzzi et Magoun (1949) sur le système réticulaire activateur ascendant du tronc cérébral: ces recherches ont mis en lumière l'importance des afférences non-spécifiques pour le maintien de la vigilance. Chez les Invertébrés, le rôle dynamogénique des stimulations sensorielles a été signalé à plusieurs reprises: par exemple, chez les Anthoméduses, les Annélides Polychètes, les Géphyriens, les Cirrhipèdes (Von Buddenbrock, 1952).

Chez les Insectes, ce problème a fait l'objet d'assez nombreux travaux, le plus souvent en relation avec l'orientation spatiale. Il existe une littérature abondante sur le rôle des ocelles frontaux dans l'orientation phototactique (cf. Cassier 1960, Médioni, 1961): il semblerait qu'il existe une "division du travail"—plus ou moins achevée suivant les cas—entre les yeux composés qui règlent la "composante taxique" de l'orientation et les ocelles qui règlent la "composante kinétique", c'est-à-dire la rapidité de la prise d'orientation et de la locomotion orientée. Certains auteurs (Bozler 1926, Goustard 1955) tendent même à considérer le "complexe oculo-ocellaire" comme un ensemble fonctionnel spécifiquement responsable du comportement phototactique dans son ensemble.

Les données qui vont suivre permettront: (*a*) de rectifier ce point de vue, en démontrant la non-spécificité de la dynamogénie ocellaire, vis-à-vis des réactions à la lumière; (*b*) de fournir des informations préliminaires sur l'existence d'une dynamogénie à point de départ antennaire. —Toutes les expériences ont porté sur l'imago mâle de *Drosophila melanogaster*.

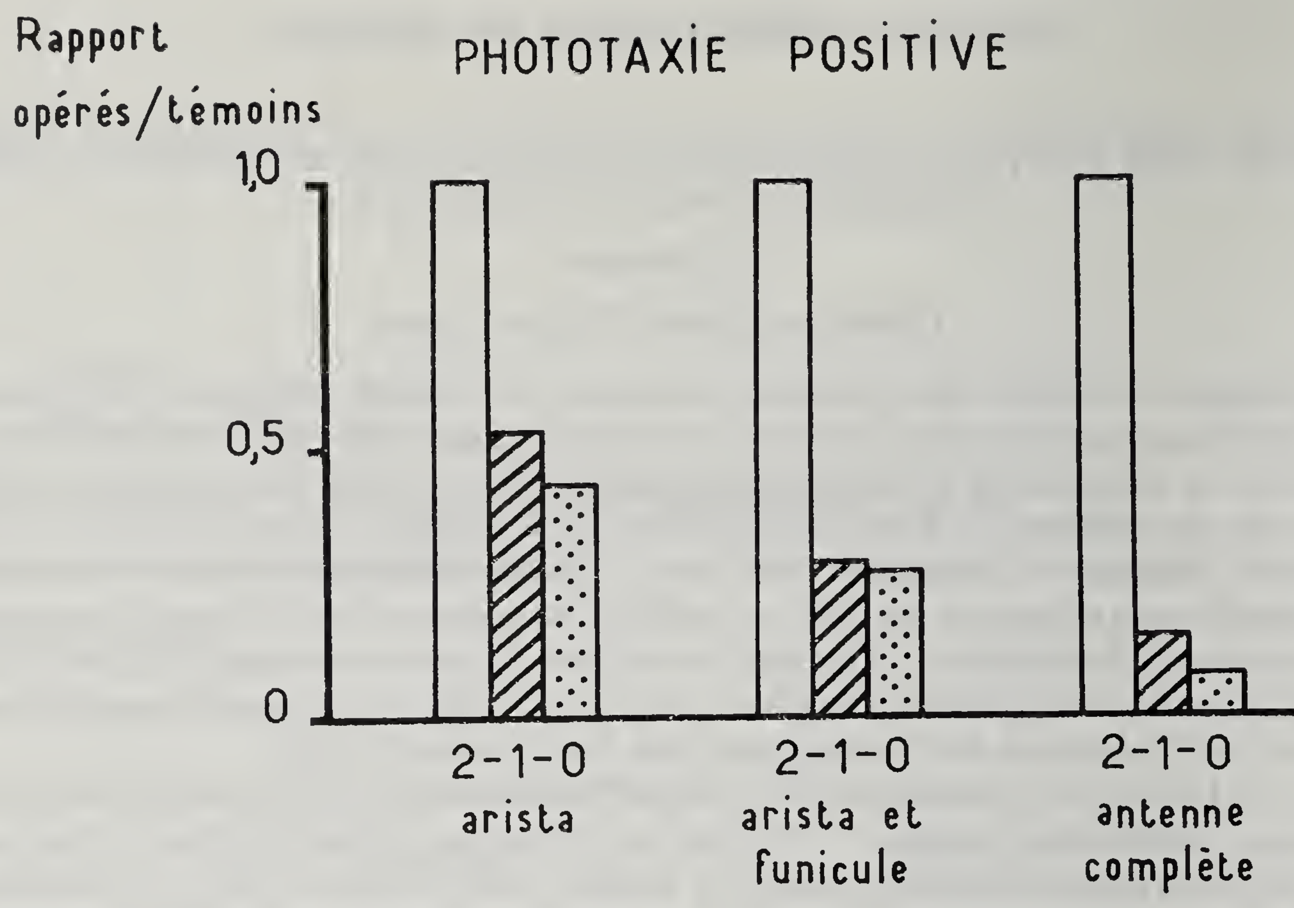
A. Non-spécificité de la dynamogénie ocellaire.

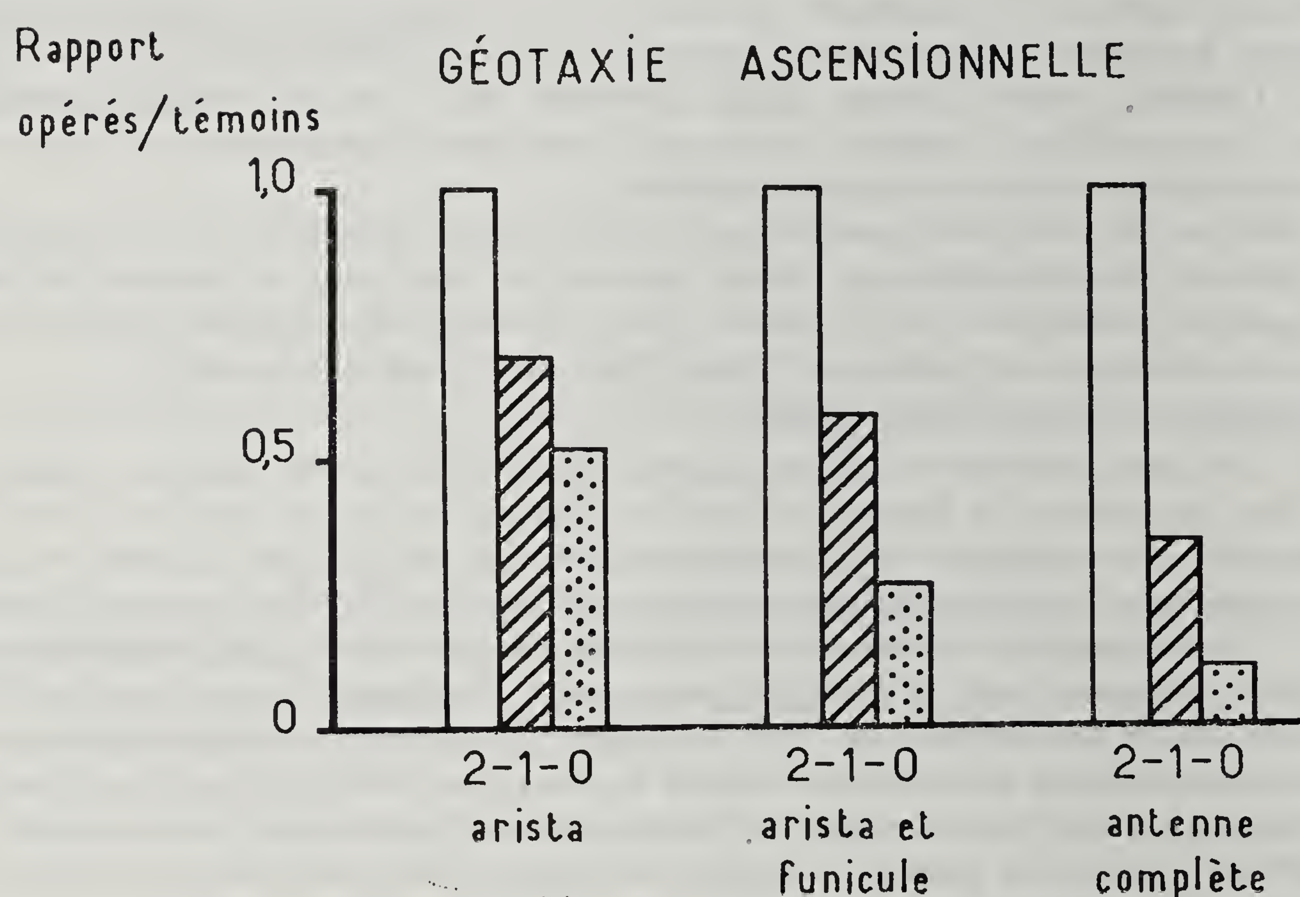
(1°) On peut démontrer la dynamogénie ocellaire dans les réactions photiques, en plaçant dans un champ de lumière dirigée des Drosophiles ayant zéro, un, deux ou trois ocelles aveuglés par application d'un vernis noir: la vitesse des parcours orientés vers la source lumineuse augmente alors systématiquement avec le nombre d'ocelles demeurés fonctionnels.

(2°) La dynamogénie ocellaire ne se limite pas à la phototaxie; elle s'étend à des réactions sans rapport nécessaire avec la lumière, par exemple la géotaxie ascensionnelle. Dans un tube vertical éclairé latéralement de façon homogène, la vitesse de grimpée est anormalement faible chez des animaux aux ocelles aveuglés ou chez des mutants dépourvus d'ocelles (Par contre, l'excitation des yeux composés ne retentit pas sur la géocinèse ascensionnelle: il n'y a pas de différence entre la vitesse de grimpée de mutants *Bar*, dont les yeux sont réduits, et celle de témoins normaux).

(3°) En milieu éclairé, le niveau de l'activité locomotrice "spontanée" dépend également de la présence ou de l'absence des afférences ocellaires: ce niveau est systématiquement plus élevé chez des témoins aux ocelles intacts que chez des animaux aux ocelles aveuglés ou chez des mutants sans ocelles. Entre 1 et 1200 lux, le niveau d'activité diminue graduellement chez les deux catégories d'animaux, mais plus rapidement chez les mutants *ocelli-less* que chez les témoins. Les yeux composés doivent donc exercer une photo-inhibition (déjà signalée dans l'analyse expérimentale de la phototaxie, Médioni 1961); mais, chez les Insectes du type sauvage, cette inhibition est partiellement compensée par une photo-activation ocellaire.

L'ensemble de ces résultats montre que la dynamogénie ocellaire, bien loin de se limiter au domaine des réactions à la lumière, stimulus adéquat de l'ocelle, retentit sur la réactivité générale de l'organisme. Même dans les réactions photiques, l'excitation des ocelles semble agir *indirectement*, par l'intermédiaire d'un mécanisme nerveux d'activation centrale, tout comme le font, par exemple, les excitations de nature vibratoire qui augmentent identiquement la vitesse et la rectitude des parcours photopositifs des Drosophiles (Carpenter 1905).





B. Rôle dynamogénique des antennes dans l'orientation phototactique positive et géotactique ascensionnelle (Recherches encore inédites de Mireille Campan, 1963).

Les ocelles frontaux des Insectes représentent un type d'organes sensoriel assez particulier: car on ne peut leur attribuer valablement de fonction perceptive précise et, en tout cas, la dynamogénie est leur fonction la plus évidente. Nous avons donc mis à l'étude, dans notre laboratoire, le problème du rôle dynamogénique éventuel d'un organe qui assure des fonctions perceptives multiples: l'antenne qui, chez la Drosophile, est importante pour le toucher (arista), pour l'olfaction et le sens de l'humide (funicule), pour la réception des vibrations mécaniques (pédicelle).

(1°) L' extirpation complète d'une seule antenne conserve toutes ces sensibilités spécifiques. Pourtant, cette opération cause une diminution importante de la réactivité à la pesanteur et même à la lumière: la géocinèse ascensionnelle et la photocinèse positive des opérés sont fortement abaissées.

(2°) L'antennectomie bilatérale complète a des conséquences encore plus nettes: les animaux ne se déplacent plus qu'exceptionnellement dans le champ gravifique ou dans le champ lumineux.

(3°) Des ablations étagées d'une ou des deux antennes causent une diminution graduée de la réactivité à la lumière et à la pesanteur.

(4°) Ces phénomènes ne sont pas la conséquence d'un choc opératoire; en effet celui-ci se manifeste 24 heures après l'opération et se dissipe ensuite graduellement; il a pratiquement disparu au moment de l'épreuve portant sur les réactions à la lumière et à la pesanteur, 72 heures après l'opération (voir figure).

Ainsi, en première approche, on peut admettre que les afférences antennaires augmentent normalement le niveau de la réactivité taxique de la Drosophile, quelle que soit leur modalité sensorielle (puisque l'ablation de *chacun* des segments antennaires diminue la géocinèse et la photocinèse). En dehors de leurs fonctions de perception, encore mal connues dans le détail, les différentes parties de l'antenne exercent donc une action dynamogénique banale, comparable à celle des ocelles frontaux. Ce fait ressort tout particulièrement de leur intervention *indirecte* dans la photocinèse, puisque les antennes ne portent pas de photorécepteurs.

Les recherches sur les fonctions dynamogéniques des organes sensoriels n'en sont encore qu'à leurs premiers débuts. Il semblerait que les Insectes puissent constituer un matériel d'étude particulièrement favorable, en raison de la richesse et de la diversité de leur équipement sensoriel, ainsi que de la relative stéréotypie de leur comportement.

REACTION OF FLYING MOSQUITOES TO VARIOUS STIMULI

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A mosquito locates and attacks its host through an essentially automatic sequence of unit responses to external stimuli. The attack program and its modification by repellents have been analysed quantitatively.

For example, *Aedes aegypti* resting in clean air fly off spontaneously at random intervals so that the decay of the resting population follows the same mathematical law as the decay of a radioactive element with a "half life" of about 45 minutes. This result was unexpected. In repellent-permeated air, the half life is reduced to about 1 minute, but the activation is still random—again an unexpected result.

Thus, resting mosquitoes are "distilled" rather than "driven" out of a repellent atmosphere. If the first mosquitoes to fly off in repellent air are collected and re-tested separately from the slower ones, each sub-group reproduces the behavior of the whole. This shows that there are no consistently susceptible or refractory individuals that can be segregated by repeated fractionation. The simplest inference is that the impulse to fly is not generated by the accumulation of some metabolic product or repellent chemical in the system, but that it results from an unusually large incidence of random action potentials in some part of the central nervous system.

High temperature or raised carbon dioxide concentration also accelerate take-off, but whether the intervals are again random has not yet been established.

From all this it is clear that simple comparisons of the relative numbers alighting—or merely congregating—in contaminated and uncontaminated air streams is not a valid criterion of intrinsic repellency, and to understand repellency we must first analyse the attack program.

With *Aedes aegypti* it starts with activation by CO_2 which excites them but does not indicate the direction of the source because it may reach the insects by a round-about path. In still air, and disregarding turns at the walls of the cage, the flight tracks consist generally of

straight segments separated by distinct turns. Quantitatively, the tendency to turn is independent of the time since the last turn, so that there is a certain basal rate of spontaneous turning which, like the flying-off behavior, is again random. Furthermore, and again unexpectedly, it is not affected by a uniformly distributed repellent vapor.

In moving air, a visually guided up-wind component may be superimposed on the random search (Kennedy, 1939).

In either moving or still air, the flight pattern changes abruptly when the mosquito encounters a convection current from an animal body. These currents can be made visible with smoke and are strong enough to be important to the insect.

In an observation chamber with two separately conditioned air streams moving upward side by side, mosquitoes tend to turn away from the air stream that is unfavourably hot, or cold, or dry, or low in CO_2, or permeated with repellent, but when moving out of the unfavorable air stream there is no tendency to turn at the boundary. Quantitatively, encounters with an unfavorable stream increase the turn rate above the basal value, but entry into a favorable stream does not reduce it below the basal value.

Thus the mosquito makes a strong turning response when leaving the convection current, but responds very little on entering it. It becomes "trapped" in the convection zone, and this is the critical phase of the attack program.

Visual and possibly infrared influences may be involved in the actual alightment.

Flight observations in a chamber fed from below with two separately conditioned air streams show two important effects of the repellent vapor: the mosquito turns abruptly on *entering* the repellent air stream, and the addition of repellent vapor to an otherwise favorable air stream inhibits the normal turn-back on *leaving* it.

Therefore, when a repellent is applied to the skin so that its vapour is added to the convection currents, the effect is to reverse the normal attack program at its two most vital points. (Any effect of direct contact between the insect and the repellent film would be additional, but is irrelevant here because our interest lies in forestalling any alightment on the skin).

We have found nothing in the normal attack program that necessarily implies the possession of an olfactory sense by *Aedes aegypti*.

Since specific responses must be caused when nerve signals arrive at particular behavior "command centers", we have tried in the following way to find out where they originate.

Steward and Atwood (1963) have described and distinguished on the antennae of *Aedes aegypti* three types of sensory setae which appear to be concerned with host finding. Types A1 and A2 are structurally similar, and we suggest that they have qualitatively similar functions as chemoreceptors for water vapor and carbon dioxide. Type A3 is structurally distinct and is probably the temperature sensor.

Steward and Atwood find that the distribution of the three types over the thirteen segments of the antennae is neither uniform nor random. Therefore, by amputating predetermined numbers of segments they changed the relative numbers of the three types of sensillae in definite ways, and could then observe how the host finding was affected.

We recalculated their data to get a mean biting rate which was plotted against the logarithm of the number of setae of each type remaining on the partially amputated antennae. The plots for A2 and A3 are straight, but for A1 it is curved. This suggests that A2 and A3 mediate host *finding* especially and detect water vapor and temperature respectively. Type A1 is probably the CO_2 sensor and only indirectly related to host finding.

Our conclusions agree generally with Slifer and Sekhon (1962) but conflict with Ismail's (1962) conclusions for *Anopheles maculipennis*. However, this is a nocturnal insect where *Aedes aegypti* is diurnal. Our preliminary experiments with *Anopheles quadrimaculatus* (another night-flying species) reveal substantial differences in the attack program and especially in the response to CO_2 which we hope eventually to correlate with the special sensory equipment of these insects.

This work was done for the U.S. Army Medical Research and Development Command.

DIE EVOLUTION DER LICHTORIENTIERUNG IN DER KLASSE DER INSEKTEN

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Alle Insekten mit gut entwickelten Augen besitzen—soweit wir wissen—die Fähigkeit, sich orientiert einer Lichtquelle zu nähern, oder sich von ihr zu entfernen. Wir sprechen im ersten Fall von einer positiven, im zweiten von einer negativen Phototaxis. Innerhalb der Pterygoten ist zusätzlich sowohl bei fliegenden Arten, wie z.B. bei Libellen (Odonata), als auch bei frei schwimmenden Formen, wie Käferlarven (Dytiscidae) oder imaginalen Wasserwanzen (Hydrocorisae) die Lichtrückenorientierung weit verbreitet. Bei den Apterygoten dagegen gibt es nach unseren bisherigen Kenntnissen noch keine Lichtrückenorientierung. Diese Orientierungsweise scheint folglich erst nach dem Erwerb der Flugfähigkeit entstanden zu sein.

Die positive Phototaxis, die negative Phototaxis und die Lichtrückenorientierung sind ihrer weiten Verbreitung wegen als ursprüngliche Typen der Orientierung von Insekten bzw. Pterygoten anzusehen. Diese drei Taxien sollen Grundorientierungen genannt werden. Differenziertere Orientierungsformen lassen sich von diesen Grundorientierungen phylogenetisch und ontogenetisch ableiten.

Bei den Insekten können wir experimentell zwei Ausprägungsformen der positiven und der negativen Phototaxis unterscheiden: Läuft ein Insekt an einer schrägen, horizontal streifend beleuchteten Wand in einer Kompromißrichtung zwischen einer Geotaxis und einer Phototaxis, dann kann sein Laufwinkel mit zunehmender Lichtstärke wachsen oder abnehmen. Ist dies der Fall, dann sprechen wir von einer Prophototaxis. Bleibt jedoch trotz variierter Lichtstärke die Kompromißrichtung konstant, dann liegt eine Metaphototaxis vor. Mit anderen Worten: Die Stärke der Wende—oder Drehtendenz auf das Licht zu, oder von ihm weg, ist im ersten Fall reizstärkenabhängig, im zweiten Fall nicht. Myriapoden, Apterygoten und die Polyneopteren verfügen alle—soweit untersucht—über eine Prophototaxis. Bei vielen Vertretern der Palaeopteren, Paraneopteren und Oligoneopteren (Holometabola) wurde mit Ausnahme von *Sialis* immer eine Metaphototaxis nachgewiesen. Aus diesen Befunden darf geschlossen werden, daß die Prophototaxis phylogenetisch älter ist als die Metaphototaxis. Die Larven einer Wanze (*Spilostethus equestris*) und von drei holometabolen Insekten (*Pteronidea ribesii*, *Inachis io*, *Tenebrio molitor*) reagierten mit einer Prophototaxis.

Eine Fülle von Befunden zeigen, daß die Photomenotaxis (= Lichtkompaßorientierung) in physiologisch enger Beziehung zu jeweils einer Grundorientierung steht. Bei der Wanderheuschrecke, *Locusta migratoria*, die über eine Prophototaxis verfügt, ändert sich z.B. auch der Menotaxiswinkel mit der Lichthelligkeit. Daher liegt die Annahme nahe, daß ein analoges Ursachengefüge sowohl die Kompromißrichtungen zwischen Geotaxis und Phototaxis als auch die Menotaxisrichtungen bestimmt. Eine Kompromißrichtung entsteht sicher durch die gegenseitige Kompensation antagonistisch wirkender, phototaktischer und geotaktischer Drehtendenzen. Bei der Photomenotaxis ist demnach zu erwarten, daß an Stelle der geotaktischen Drehtendenz eine spontane Drehung (Drehtendenz) die Drehtendenz einer Grundorientierung kompensiert (= Kompensations—theorie der Menotaxis). Zugunsten dieser Deutung der Menotaxis gibt es viele Belege. Am überzeugendsten wurde die Kompensationstheorie der Menotaxis von Schöne (1962) an den Larven von Dytisciden belegt. Bei diesen Larven wirkte eine spontane Dreherregung entgegen einer Drehtendenz der Lichtrückenorientierung als Grundorientierung. Viele holometabole Insekten (z.B. *Formica* und *Apis*) besitzen im Einklang mit dieser Theorie eine Metaphototaxis und eine helligkeitsinvariante Photomenotaxis.

Zahlreiche holometabole Insektenarten (Formicidae, Carabidae, Vespidae usw.) können sich photomenotaktisch in eine bestimmte Himmelsrichtung orientieren, indem sie die Wanderung der Sonne durch eine entsprechende zeitabhängige Gegendrehung kompensieren. Diese Form der Orientierung wird astronomische Orientierung oder Astrotaxis genannt. Es ist anzunehmen, daß allen Insekten mit einer Prophototaxis die Fähigkeit der Astrotaxis fehlt, da wahrscheinlich alle diese Arten keinen festen Menotaxiswinkel beibehalten können, wenn sich die Lichtintensität ändert. Ameisen und Bienen erlernen die Fähigkeit der Astrotaxis nur, wenn sie länger zwischen Nistplatz und Sammelstelle pendeln. Da den ursprünglichen

Hymenopteren (Symphyta, Terebrantia und einigen Aculeata) ein fester Nistplatz fehlt, ist es sehr wahrscheinlich, daß bei den Hymenopteren die Fähigkeit der Astrotaxis erst innerhalb dieser Ordnung entstand. Einige Käfer (Carabidae, Tenebrionidae, Staphylinidae) zeigen die Fähigkeit der Astrotaxis. Sie ist ihnen wahrscheinlich angeboren, da diese Insekten wohl kaum zwischen zwei Punkten längere Zeit pendeln wie Bienen und Ameisen.

Eine weiters komplexe Form der Orientierung, die Telotaxis, ist unter den Insekten weit verbreitet: Biologisch wichtige Objekte, wie Lichtpunkte, dunkle Löcher, Blüten, Beutetiere usw. werden gezielt angeflogen oder angelaufen. Charakteristisch für die Telotaxis im weiteren Sinn sind drei Handlungsphasen: 1. Das Absuchen der Umgebung nach Objekten durch Drehbewegungen auf der Stelle oder während der Fortbewegung. Zwei ähnliche Objekte werden oft alternativ fixiert, was sich in Zick-Zack-Läufen äußert, wenn sich das Insekt gleichzeitig fortbewegt. Es ist anzunehmen, daß beim alternativen Fixieren die Objekte miteinander verglichen werden. 2. Das erwählte Objekt wird endgültig fixiert und damit die optische Suchbewegung unterbrochen. Schlüsselreize des Objekts müssen diese Handlung auslösen. 3. Das fixierte Objekt wird orientiert angelaufen.

Von Ameisen (*Formica rufa*), Skorpionen (Buthidae) and Maikäfern (*Melolontha melolontha*) ist bekannt, daß sie sich während der gezielten Bewegung auf eine dunkle Fläche am Horizont die Stellung einer Lichtquelle (z.B. die Sonne) in beliebiger Richtung merken und als Bezugsreiz für eine Menotaxis zum Zielort verwenden. Mit Hilfe dieser Menotaxis ist es möglich, daß die eingeschlagene Zielrichtung auch dann noch beibehalten werden kann, wenn das Zielobjekt vor-übergehend nicht sichtbar ist. Es ist noch nicht bekannt, ob bei allen Insektenarten in dieser dritten Phase der Telotaxis eine Menotaxis eingesetzt werden kann.

Die Schlüsselreize, die gezielte Bewegungen auf Figuren auslösen, sind jeweils den speziellen biologischen Bedürfnissen angepaßt: Bienen und Hummeln z.B. bevorzugen bei der Futtersuche aufgelöste, bei der Nestsuche geschlossene, schwarze Figuren. Raupen und viele andere Pflanzenbewohner zielen auf vertikale, dunkle Streifen, was das Auffinden der Futterpflanzen erleichtert. Unter Steinen lebende Arten wie *Gryllus bimaculatus* (Gryllidae) und *Buthus occitanus* (Scorpiones) sprechen besonders auf waagerecht sich erstreckende Flächen in Horizontnähe an.

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LIGHT RESPONSES OF THE TWO-SPOTTED SPIDER MITE *TETRANYCHUS URTICAE* KOCH (ACARINA; TETRANYCHIDAE)

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Light responses of female two-spotted spider mites were investigated in relation to nutrition and humidity conditions. Results indicate that starvation produces in the mite "a state of capability" to develop a light response. This "state of capability" is apparently differentiated according to the degree of starvation so as to facilitate responses of different sign and possibly of different kind in a fixed order (fig. 1). However, the response is demonstrated or not according to humidity conditions (Table 1).

The intensity of the negative response seems independent of the magnitude of the difference between the perception and the accommodation humidities. But the duration of the period, when the negative and the compass light reactions are demonstrable seems to depend on the time that is necessary to accommodate the humidity receptor(s) to the perception humidity. All this is probably superimposed on another relationship, in which high environmental humidities facilitate akinesis and supress positive light responses, while low environmental humidities facilitate the dispersal tendency and positive light response of the mite.

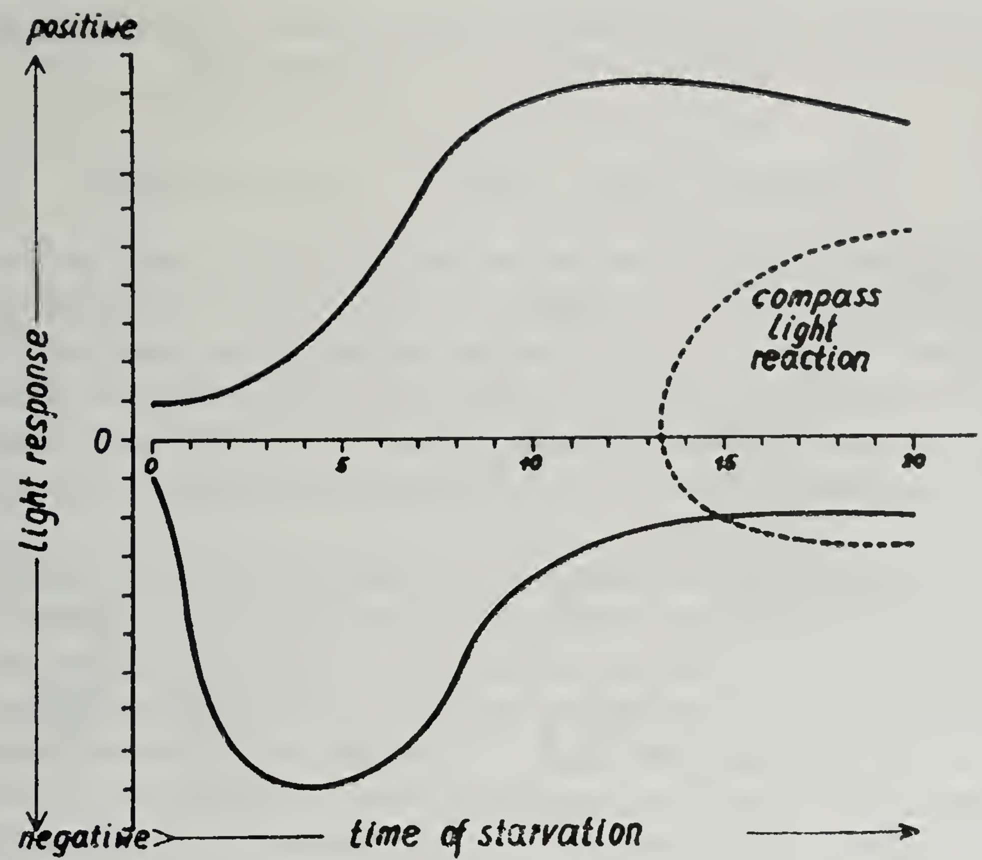

FIG. 1. Light responses of *Tetranychus urticae*

It seems that the above described behaviour patterns are evolutionary adaptations to use light as a token stimulus in the search for food.

Satiated mites respond indifferently to light regardless of humidity conditions. In the first phase of starvation the search for food is probably limited to the closest neighbourhood, for instance the same plant. The pattern consisting of random search and a negative light response is here probably quite effective, because a higher humidity and a deeper shadow are usually associated with transpiring leaves in foliage. Prolonged starvation (the second phase) causes mites to leave the host plant, completely deprived of food reserves. The positive light response enables the animal to find the most suitable place from which to sail on a silk thread in convection currents. When the sailing thread ultimately hooks on to an obstacle, the negative and/or the positive light responses develop according to humidity conditions. This behaviour ultimately results in satiation or in a further journey. In the third starvation phase an indifferent or a compass light reaction substitute the negative response. These two responses probably increase the chance of survival of the population at the cost of decreased survival of individuals.

TABLE I

Starvation phase	*Humidity conditions*	*Light response*
I (0 to 3-5 hrs.)	Prc.h.[a] ≦ Acc.h.[b]	indifferent
	Prc.h. > Acc.h.	negative
II (3-5 to 7-10 hrs.)	Prc.h. ≦ Acc.h.	positive
	Prc.h. > Acc.h.	negative
III (7-10 to 20 or more)	Prc.h. ≦ Acc.h.	positive
	Prc.h. > Acc.h.	indifferent or compass light reaction

(*a*) Perception humidity, i.e. the humidity to which an individual is subjected at the particular moment.

(*b*) Accommodation humidity, i.e. the humidity to which an individual became accommodated in its recent history.

THE ORIENTATION OF *MELANOPHILA ACUMINATA* DEGEER (COLEOPTERA, BUPRESTIDAE) TO FIRES

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The attraction of *Melanophila acuminata* to forest fires is related to the ovipositional behaviour of this species since the females deposit their eggs in fresh fire-killed conifers. Antennal temperature receptors are utilised for orientation purposes near sources of heat but infra-red receptors on the meso-thorax (1) function as long-distance detectors of radiation given off by fires. During flight the meso-thoracic sense organs are completely exposed but when the insect is walking the middle legs interfere with reception, so these organs must function during flight.

By subjecting this species to brief exposures of infra-red radiation in a spectrophotometer, reactions were obtained in the wavelength region of 2·0 to 6·5 microns. These reactions consist of a definite twitch of the antenna when the radiation is focused on the mesothoracic sense organs. The lowest energy perceived was $0{\cdot}6 \times 10^{-4}$ watts per square centimeter at a wavelength of 4·0 microns, but a rather high wavelength sensitivity was recorded over the 3·5 to 4·5 micron range. This range corresponds to the wavelengths of peak radiation from burning wood in forest fires. It also coincides to a degree with a "window" in the atmosphere which is transparent to infra-red radiation. This window in the region of 3·6 microns to 4·1 microns along with other "windows" occurs between regions of high absorption of radiation by carbon dioxide and water. Only about eight per cent of the total radiation from any heat source is transmitted through the 3·6 to 4·1 micron "window". This energy is further attenuated at any distance since the total radiation received is inversely proportional to the square of the distance from the source. The radiation also varies as the cosine of the angle between a detector and a line perpendicular to the surface of the heat source. By taking all these factors into consideration, a series of curves can be plotted which show the sizes of forest fires that could be perceived by *Melanophila* at various distances and at different angles of sight, based on the threshold value of $0{\cdot}6 \times 10^{-4}$ watts per square centimeter. For example, a fifty acre fire, consisting of glowing wood embers with an average temperature of 800°F., could be detected by *Melanophila* at a distance of six kilometers away when the insect is at an angle of 45 degrees to a line perpendicular to the surface of the fire. Actively burning fires would be detected at greater distances because of their greater intensity of radiation.

The receptors could function tropotactically or even telotactically to bring these insects near a source of heat. Once at the fire the antennal sense organs probably function to control the movements of the insects so that they are not overcome by the flames. The infra-red receptors are not needed at a fire so they could only function as long-distance receptors of radiation. More detailed results will be published in the *Canadian Entomologist*.

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CONDITIONS OF NESTING SITES WITH REFERENCE TO SPATIAL ORIENTATION IN *BEMBEX ROSTRATA* (L.) (HYMENOPTERA; SPHEGIDAE)

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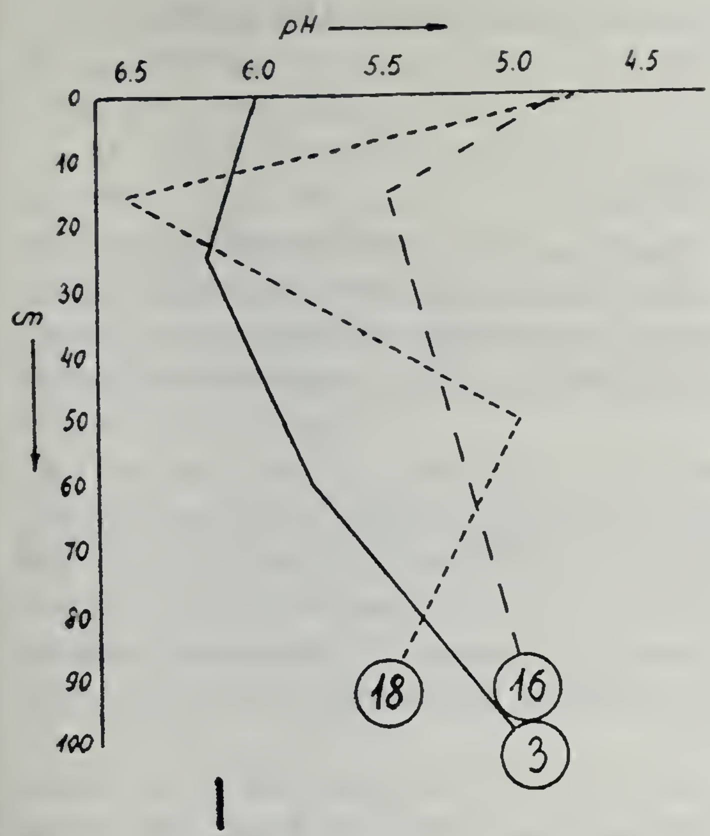
There is a close relation between the nesting site of insects and their orientation. Many insects, among them *Bembex rostrata*, show attachment to the habitat. Probably, the ecological conditions of their nesting sites exert an evolutionary influence on the survival of specimens endowed with preferences toward the appropriate nesting site. On the other hand, learning plays an important role in homing. Memory of the environment develops as soon as the insect emerges from the pupa and, for the first time looks around its habitat. Thus the



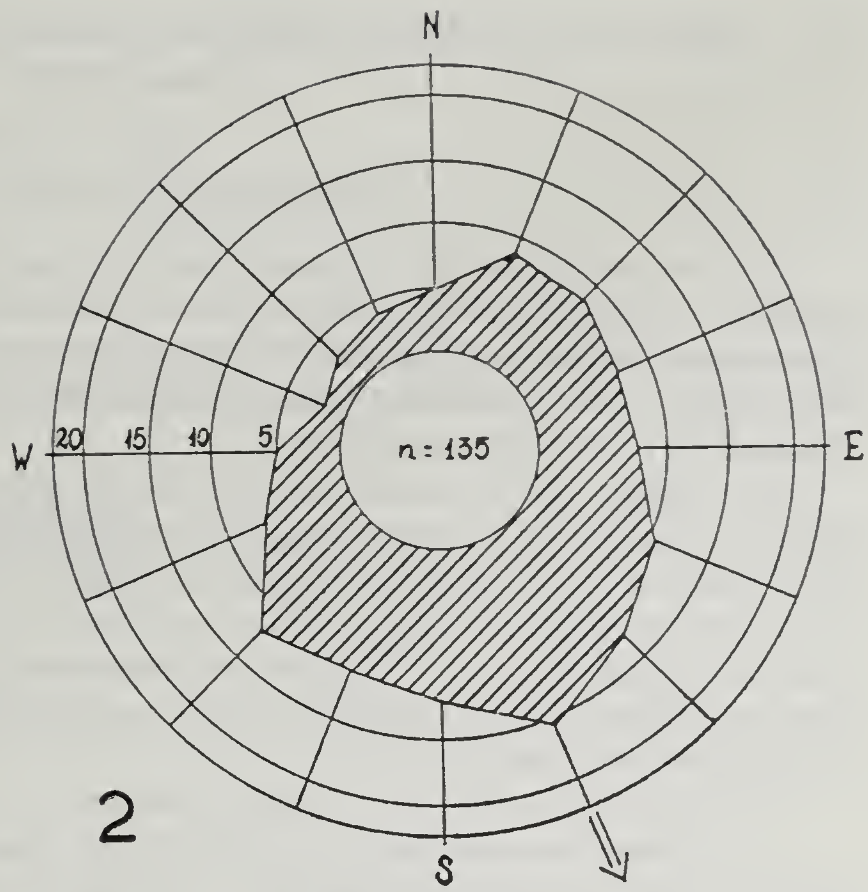


FIG. 1. Profiles of acidity of the soil in three *Bembex rostrata* nesting sites.

FIG. 2. Orientation pattern of nest entrances.

preferences shown by a female when she searches for a nesting site have important consequences for her and her offspring's orientation.

We studied these preferences by investigating the ecological characteristics of established nests of *Bembex rostrata*.

An analysis of 20 nesting sites from the region of Warsaw was carried out. Nests were always found in open barren areas lacking trees and bushes, and without shadow. Plant cover of the ground, i.e. lichen-moss and annual herb-grass stages, must not be greater than 80%; it usually does not exceed 60% in the vicinity of nest. The sites are near coniferous or mixed forests, and belong to the associations *Corynephoretum canescentis* and *Festuco-Thymetum serpylli*, characteristic of dry open sandy areas.

Results of the soil analysis are in full conformity with this. *Bembeces* nest in medium dry and dry sand, sandy loam, or loamy sand, i.e. medium loose or loose soil with 38 to 44% pore space. These features of the habitat can easily be detected by the female by touch, an open sunny clearing or field road can be chosen by sight. On the contrary, no attention is paid to the pH of the soil. This is shown by the pH profiles from the vicinity of three *Bembex* nests (fig. 1).

Some ethological implications concerning spatial orientation arise from these preferences. Nesting in open areas can be considered a condition, due to which homing of *Bembex* shows uniformity: there is little difference between the mechanism of distant and proximate orientation. A closed nest entrance is found by touch, as a spot with looser soil, showing a connection with the kind of habitat prefered by *Bembex* females.

There is also one interesting point concerning the nesting behaviour of *Bembex rostrata*. From the graph of the angular distribution of 135 nest entrances plotted in relation to compass direction (fig. 2) one can see a preference to SSE ($P < 0{\cdot}025$) which is probably connected with the direction of ground inclination preferred for nesting. Generally, there is a close correlation between the directions of orientation of nest entrances and the directions of ground inclination.

SPATIAL ORIENTATION OF *ANARETE* SP. NEAR *FELTI* (DIPTERA, CECIDOMYIIDAE)

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An earlier paper (1) reported that the midge, *Anarete* sp. near *felti* Pritchard may be induced to swarm with a marker, namely a sheet of white paper against a dark background. The swarm was formed usually 1-2 inches above the edge of the marker nearest the sun, or the front edge. This was true whether the sun changed its position or the surface of the marker changed its orientation to the sun.

To explain this phenomenon, the following hypothesis is proposed. As the incident rays strike the marker at a certain angle, the major reflection leaves the marker at the same angle. The space at 1-2 inches above the rear edge is in the path of the major reflection, and that above the front edge is in the minor and random reflection resulted from the uneven surface structure of the marker. The fact that the swarm is found only above the front edge suggests that the midges were attracted to minor and random reflections, and avoided the path of the major reflection (fig. 1A).

This hypothesis has been proved valid by a number of experiments as described below.

1. When two markers were placed one closely behind the other, the front edge of the second marker attracted no swarm. This edge was then in the path of the major reflection of the front marker (fig. 1B). However, when the second marker was moved further away, so that its front edge was beyond the major reflection of the first marker, a second swarm appeared above the front edge (fig. 1C).

2. As just mentioned, only one swarm was formed when two markers were placed one closely behind the other. But if the entire arrangement was tilted so that the angles of incidence and reflection were sharper, a swarm formed above the front edge of the second marker. This position was then out of the path of the major reflection (fig. 1D).

3. When the arrangement in fig. 1D was later slowly lowered to the horizontal position, it was observed that the midges at the upper portion of the second swarm (f_2) moved to join the first swarm (f_1). With further lowering of the markers, other midges moved forward. Since the path of the reflection moved downward as the markers were tilted back to the horizontal position, the effect of the reflection reached the midges in the upper portion of the swarm first.

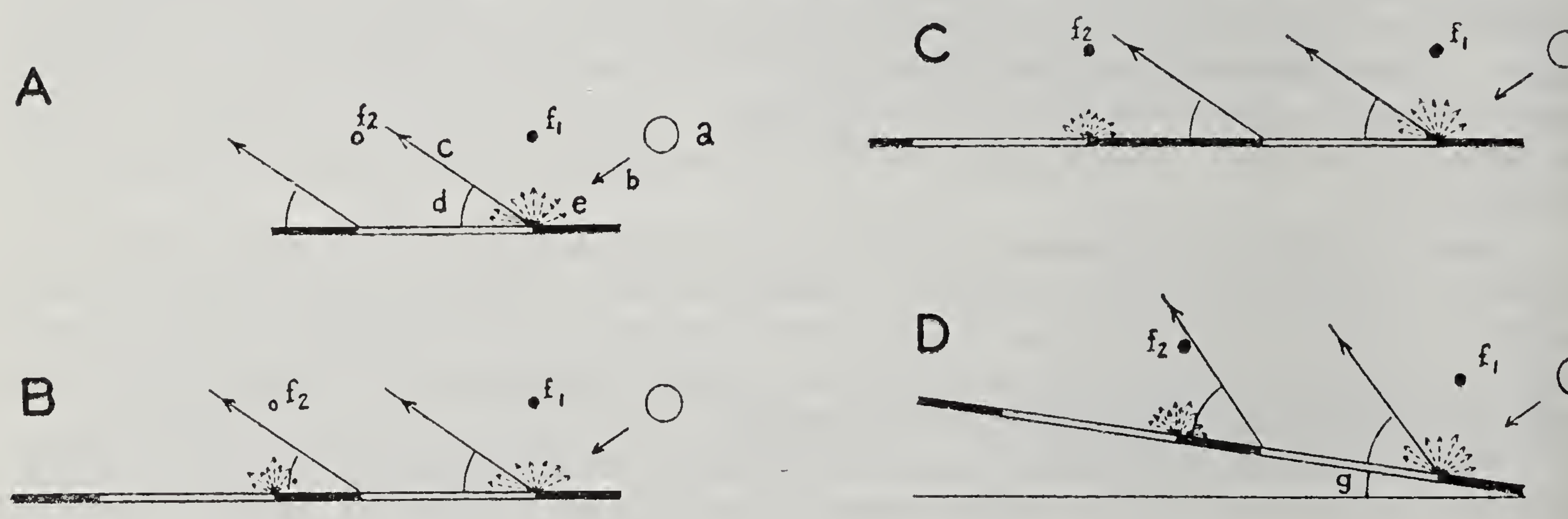

Fig. 1. Studies on the relation of reflection and midge swarms. The horizontal base in all diagrams represents the marker, with the white portion of the marker in white, and dark background in black. All diagrams represent the view parallel to the marker. (*a*) the sun, (*b*) the direction of the sun's rays, (*c*) the direction of the main reflection, (*d*) the angle between the main reflection and the marker, (*e*) the random reflection, (*f*) the location of swarms, solid dot indicates the presence of a swarm, small circle indicates the absence of swarm, (*g*) tilting of the markers.

4. The arrangement in fig. 1B normally attracted no second swarm (f_2) but it did when the general lighting intensity was lower. It is logical to infer that with lower lighting the reflection was weaker and interfered less.

5. With a mirror in the place of the white paper, no swarm was formed at all. The reflection from the mirror was concentrated at a single angle. There was no minor and random reflection above the front edge.

6. When a single marker was placed so that its surface was perpendicular to the sun's rays, the midges either dispersed or formed a very loose swarm, i.e., they flew about covering the entire marker. Under this situation, the area above the entire marker was in the path of the direct reflection.

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CONTROL OF BEHAVIOUR BY CHEMICAL AGENTS OF BIOLOGICAL ORIGIN

PHEROMONES AND MATING BEHAVIOUR

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Females of most species of moths, some Coleoptera, Hymenoptera and Blattaria attract their males by emitting an odorous substance. Experiments in the cockroach *Leucophaea* show that the female's responsiveness to the male odour can be influenced by the corpus allatum hormone acting directly on the central nervous system, thus affecting the animal's behaviour.

HORMONAL INFLUENCES IN LOCUST MARCHING BEHAVIOUR

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One of the most arresting features of locust phase change, especially in the behavioural sense, can be its rapidity. For example, solitary locust hoppers, placed in a crowd of gregarious hoppers, learn by habituation in a few hours to behave like the latter, and within a few days begin to perform as well as their gregarious colleagues both as regards speed and duration of marching. It is also easy to demonstrate that solitary and gregarious hoppers under identical stimulus conditions behave differently. One of the first implications of this might be that the sensory receptor mechanisms differ as between the phases so that the differential behaviour demonstrated in an identical stimulus situation is due to a different appreciation of that situation. On the contrary, all the experimental evidence indicates that the receptors of both phases are the same and that in an identical stimulus situation inputs to the central nervous systems would be the same in both phases.

Carlisle and Ellis (1) suggested that the behavioural differences between phases are controlled by the interaction of the secretions of more than one endocrine gland.

Haskell and Moorhouse (6) put forward the hypothesis that while the information input to the central nervous system was the same in both phases, the output differed as a result of a controlling mechanism which was responsive to phase changes; they further suggested that this mechanism might be a hormone balance. Such a system could have a response time sufficient to mediate rapid changes of phase.

The present paper outlines current research at the Anti-Locust Research Centre concerning the influence of changes in hormone balance on the marching behaviour of locusts.

Both *Schistocerca gregaria* and *Locusta migratoria migratorioides* have been used in this work and results to date indicate that the same general systems apply in both cases so that for the rest of this paper the term "hopper" or "adult" will be used to indicate both these species unless otherwise stated.

Irrigation of the nervous system of mature adult locusts with blood from a 5th-instar hopper within 12 hours of the moult produced an increase in the electrical activity in the central nervous system while it greatly reduced the activity in certain motor neurones, particularly those serving muscles of the legs. In contrast, blood taken from a hopper in mid-instar had little or no effect. This suggested that a substance was present in the blood near the time of the moult that could cut off or reduce locomotor activity, which is an observed behavioural phenomenon in locust hoppers nearing ecdysis. Since a substance necessarily present in the blood at the time of the moult is the moulting hormone, ecdyson, which is produced by the prothoracic gland, homogenates of this gland were used in experiments and found to produce the same effects when used in physiological quantities.

Ellis and Carlisle (5) found the prothoracic gland was always much larger and better developed in solitary than in gregarious locusts and in the former persists functionally in adults until at least after the first oviposition, whereas in gregarious animals it disappears at the adult moult. Carlisle and Ellis (2) showed that injection of prothoracic gland homogenates equivalent to one 5th-instar gland, into gregarious hoppers reduced marching in the experimental animals by some 40% after two hours. The effect wore off and 24 hours later marching behaviour, in both experimental and controlled insects, was normal. This finding was consistent with the physiological work and suggested that the level of marching of hoppers was in some way related to the titre of the ecdyson in their blood.

The pattern of locomotor activity throughout an instar (3, 4) closely follows the change of ecdyson level in the blood. The activity just after the moult is nil, rapidly rising to a peak in mid-instar, after which it gradually declines until near the moult it stops; in general, ecdyson titre in the blood fall off rapidly after the moult and begins to build up after the middle of the instar. The fact that the prothoracic gland is larger and more persistent in solitary locusts suggests that in that phase the ecdyson blood titre will be consistently higher than in gregarious phase insects and this may be a factor contributing to the recorded behavioural differences.

Clearly, however, this mechanism is only part of a much more complex variation which

has to be able to accommodate, for example, the daily variation in marching behaviour and also alterations of behaviour correlated with phase change.

Further neuro/humoral mechanisms are needed in the system and these should preferably be such as could be activated rapidly by external sensory stimuli, as for example when solitary hoppers are crowded. One obvious candidate for examination was the pars intercerebralis/corpus cardiacum system, and the influence of this system on marching has been investigated. *Locusta* hoppers were injected with homogenates of corpus cardiacum derived from early 5th-instar hoppers; for controls saline injections were used. After injection of one whole gland complement the recipient hopper showed an increase in marching behaviour after two hours; the effect began to wane after 4 or 5 hours and the hopper was normal again in 24 hours. Injections of a double gland complement, however, were inhibitory to marching behaviour. Injections of the gland stimulated marching only in well-fed gregarious hoppers; if starved hoppers were used the effect on marching was variable but it tended to be inhibited, while the homogenates had no action on the marching behaviour of solitary phase hoppers. Physiologically, irrigation of the central nervous system by homogenates of corpus cardiacum produced an increase of activity in the central nervous system, as with prothoracic gland hormone; in gregarious mature males of *Locusta* the electrical activity of the neurones serving the leg muscles also showed increased activity after corpus cardiacum irrigation. These findings are consistent with the idea a corpus cardiacum substance acts as a stimulus for marching, at least in *Locusta*.

The question arises as to whether ecdyson, which is in general inhibitory to marching, and the corpus cardiacum substance which is in general stimulatory, are directly antagonistic. Experiments conducted so far have given variable results but it seems that when both substances are present together the general electrical activity in the central nervous system is lower than when either substance is applied alone.

The present work must be regarded as preliminary since the techniques are crude and very inexact. Nevertheless, the approach seems promising from the qualitative point of view and the way in which it explains certain aspects of phase change encourages us to believe that it is at least representative of a major system which operates in this complex biological phenomenon.

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DIE TOTE KÖNIGIN ALS FAKTOR IM VERHALTEN UND IN DER EIERSTOCKENTWICKLUNG VON ARBEITSBIENEN IM KLEINVOLK VON *APIS MELLIFICA* L.

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Die Resultate vieler experimenteller Forschungen zeigen, dass in kleinen Gruppen von Bienen und auch in kleinen Bienenvölkern die tote Königin bzw. ihre Pheromonen inhibitorische Wirkung auf den Aufbau von Weiselzellen und auf die Eierstockentwicklung der Arbeitsbienen haben.

In der vorliegenden Arbeit wurde der Einfluss der toten Königin, die zwei Jahre vorher getötet worden war, auf das Verhalten der Arbeitsbienen und auf die Entwicklung ihrer Eierstöcke geprüft. Der Einfluss solcher Königin wurde 3 bis 5 Monate hindurch fortlaufend und ohne Unterbrechung erforscht.

Für insgesamt sechs durchgeführte Versuche, mit denen allen anfangs Juni begonnen wurde, wurden Kleinvölker von 500 Bienen verwendet. Die Versuchsbienen waren vom 4. Tag ihres Lebens an bis zum Ende der Versuchszeit im Kontakt mit je einer zwei Jahre zuvor durch Einfrieren im Kühlschrank getöteten Königin. Vom. 6. Tag ihres Lebens an kommuni-

TABELLE

FIXIERUNGSTAG UND ALTERSTAG DER BIENEN	DIE PROZENTSÄTZE DER BIENEN MIT UNAKTIVIERTEN EIERSTÖCKEN IN DEN VERSUCHEN I-VI.					
	I	II	III	IV	V	VI
4. VII 1963. 28	48	74	90	76	92	92
1. VIII 1963. 56	46	44	54	96	62	70
29. VIII 1963. 84	64	36	42	92	48	72
26. IX 1963. 112	46	20	32		52	

zierten die Arbeitsbienen frei mit ihrer Umgebung. Für die Versuche wurden einwabige Beobachtungsstöcke mit Rahmen von je 11 × 13 cm Grösse verwendet.

Zur makroskopischen Untersuchung der Eierstöcke wurden jeweils 50 Arbeitsbienen in 70 %-igem Alkohol fixiert, und zwar in Zeitabständen von 28 Tagen. Die Resultate sind in der Tabelle angegeben. Bei den am 26. IX. fixierten Arbeitsbienen fehlen die Prozentsätze der Bienen mit unaktivierten Eierstöcken für die Versuche IV und VI, weil der Versuch IV schon am 12. IX. beendet wurde, da die Zahl der Bienen dieses Volkes jäh sank, während in dem Versuchsvolk VI am 26. IX. nur drei Bienen gefunden wurden. Der Versuch II wurde am 27.IX. beendet. Die übrigen Kleinvölker hielten sich bis zum 8.X. (Versuche I, V) und bis zum 24.X. (Versuch III).

Ergebnisse.—Ein kleines Bienenvolk von 500 Arbeitsbienen hält sich 3 bis 5 Monate lang in Anwesenheit einer toten Königin, die 2 Jahre zuvor getötet wurde. Diese ganze Zeit hindurch war die Königin attraktiv für die Arbeitsbienen, und der Kontakt mit Fühlern und mit der Zunge dauerte ununterborchen an.

Die tote Königin verhindert nicht den Bau von Weiselzellen. In jedem Versuchsvolk hielten sich ein bis zwei Weiselzellen bis Ende August.

Der Entwicklungszustand der Eierstöcke bei den fixierten Arbeitsbienen, ausgedrückt in Prozentsätzen der Bienen mit unaktivierten Eierstöcken, zeigt, dass die tote Königin auch nach zwei Jahren noch einen inhibitorischen Faktor darstellt (Tabelle). Die Prozentsätze der Bienen mit solchen Eierstöcken sind verschieden, liegen jedoch, mit Ausnahme von drei Gruppen, in keinem Fall unter 40%. In einigen Gruppen bewegen sie sich sogar zwischen 70 und 92%. Bei der Gesamtzahl von 1.100 in allen Versuchen fixierten Arbeitsbienen betrug der Prozentzatz der Bienen mit unaktivierten Eierstöcken 61%.

Bei allen Versuchen, ausgenomen Versuch II, kam es zum Auftreten funktioneller Afterköniginnen, doch in sehr beschränkter Zahl. Die Drohnenmütterchen legten nur in 1 bis 2 Weiselzellen Eier, und zwar je ein Ei auf den Boden der Zelle, während sie in die Zellen der Arbeitsbienen, ausgenommen Versuch IV, keine Eier legten. Die hemmende Wirkung der toten Königin beeinflusst auch die gesellschaftlichen Funktionen der Arbeitsbienen.

IN-FLIGHT DISPERSAL AND ORIENTATION OF TWO *SCOLYTUS* SPECIES (COLEOPTERA) TO THEIR HOST PLANTS FOR OVIPOSITIONAL PURPOSES

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This paper presents our recent findings in studying the dispersal and orientation of *Scolytus multistriatus* (Marsh.) to *Ulmus* and *S. quadrispinosus* Say to *Carya.*

These beetles are characterised by (1) feeding in twigs of healthy trees for sexual maturation and (2) subsequent attack for oviposition in the trunk and larger branches of declining trees. Thus, two orientation phenomena were studied in relation to the host.

Emergence from brood wood. The threshold air temperature for emergence of *S. multistriatus* from brood wood ranged from 15-18°C, and from 21-23°C for *S. quadrispinosus.* Emergence occurred normally in complete darkness.

Initiation of flight dispersal. Beetles showed a negative geotropic response in the selection of a flight "take-off" site. This was especially the dominant behavior when the air temperature was near the threshold range for initiation of flight, about 22-23°C.

Flight "take-off" was random in direction under uniform illumination, but usually toward the greatest illumination in broken shade.

In-flight dispersal behavior. Once in flight, beetles usually initially flew "with the wind" if the air velocity gusted over 5 m.p.h. In conditions of less air velocity, initial direction was erratic. The height of beetle flight in an oak-hickory wood was mostly above the undergrowth vegetation. The upper limits of flight elevation were not studied.

Preliminary studies indicated that *Scolytus* beetles are not attracted to healthy hosts, but arrive at such trees by random dispersal.

Once in contact with the twigs of the host the beetles were stimulated to feed. In the case of *S. multistriatus,* this choice of a feeding site was governed by thigmotactic stimuli, such as angle of twig branching, and the presence of chemical locomotory arrestants and feeding stimulants in elm bark. Over 90 per cent of such feeding by *S. multistriatus* was in 2nd to 4th year growth until current growth became woody in late June. With *S. quadrispinosus* twig feeding was predominately in current growth. This beetle also showed a consistent feeding preference for *Carya ovata* over *C. cordiformis.*

Beetles dissected from newly initiated-feeding scars in twigs consistently had immature ovaries. After feeding for 10-15 days in such twigs, beetles had fully mature ovaries.

Attraction to hosts for oviposition. Sexually mature beetles were subsequently attracted to deteriorating host material. The larger the volume of host wood the more attractive, if other conditions were standardised. The attractiveness of a fixed volume of host, maintained free of attacking beetles, decreased during the interval from 7 to 14 days after girdling the tree. Female beetles initiated galleries in such host material, and 98·4 per cent of 244 examined galleries were initiated over phloem rays. This highly consistent behavior pattern in the location of the gallery entrance was probably determined largely by an optimal concentration of the feeding stimulants in phloem ray tissues.

The presence of females in galleries in host wood supplemented the beetle attraction to the host. The magnitude of attraction by the beetle-associated factor was positively correlated (within limits) with the number of females making galleries in a fixed volume of bark.

The attractant of deteriorating host tissue and the host contribution to the beetle-associated attractant were both present in bark.

CONTROL OF THE ORIENTATION AND FEEDING BEHAVIOUR OF RED COTTON BUG, *DYSDERCUS KOENIGII* (F.) BY CHEMICAL CONSTITUENTS OF PLANTS

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Dysdercus koenigii prefers to feed on certain malvaceous plants, particularly cotton (*Gossypium* spp.) and okra (*Abelmoschus esculentus*), rather than on non-malvaceous plants. The insect feeds on succulent parts like leaves, unripe green fruits, only when it is desiccated; normally it feeds on mature dry seeds in the dehisced fruits.

This discrimination is governed to a large extent by the presence or absence in the plants of certain specific chemical compounds, operating as follows:

1. In the first stage, an aromatic fraction of the ether extract of cotton leaves attracts the insect from a short distance and prevents it from moving away. Such a chemical stimulus is wanting in non-malvaceous plants. The chemical stimulus from the leaves of cotton plants serves as an olfactory attractant and it does not induce the insect to feed on the leaves. On the other hand, high water content of the leaves stimulates ingestion of the sap by the insect if the latter is desiccated. If the insect's water content is high, it avoids high humidity zones in search of dry zones which it finds in the dehisced, dry, fruits of the plants.

2. Once the insect comes within a distance of about a centimetre from the mature seeds in the dehisced fruits, an olfactory stimulus from the seeds draws the insect towards them and stimulates extension and application of the proboscis to the seeds. This stimulus is provided by certain lipids which have been fractionated, separated and tested on paper chromatograms. Such an olfactory stimulant is present in, besides cotton, a few other malvaceous but not in non-malvaceous seeds. However, the intensity of the attraction and feeding responses of the insect to this chemical stimulus declines with desiccation which increases its response to water-stimulus.

3. Once the proboscis is applied to the seeds, chemicals of the third category stimulate the gustatory receptors at the tip of the labium. These chemicals include mainly sugars like sucrose, glucose and raffinose and they are of general occurrence in many plants (not raffinose). Stimulation by the gustatory chemical stimulants causes the stylets' insertion into the inner tissues of the seeds and ingestion of its constituents. The same chemicals are also responsible for stimulating the epipharyngeal gustatory receptors causing continuation of the process of ingestion of food.

It may be concluded that certain specific chemical constitutents of the leaves and seeds of certain malvaceous plants, and not the gustatory stimulants like sugars present in the seeds of many plants, are responsible for the preference for feeding on malvaceous plants. The intensity of response to such specific chemical stimuli from the plants is influenced to a large extent by the water content of the insect, and the period of its starvation.

THE HOUSEFLY AND THE CUBE OF SUGAR

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In his investigations on the "fly factor" in the housefly, Wiesmann (1) used 3-day-old flies kept on sugar and water. In view of the strong difference in attraction between male and female houseflies (2), we explored "fly factor" and herd instinct on sugar in cages of the two sexes, as well as at different ages.

In mixed populations we could fully confirm Wiesmann's findings on the fly "factor". The same held true for the herd instinct on sugar.

Cubes of sugar attract females much more strongly than males. This is evident at all ages, but seems less pronounced in the first four days of life. The same effect is obtained by using dry paper strips, on which sugar had been crystallised.

There is, in general, a stronger attraction to "fly sugar" (i.e. contaminated with the "fly factor") than to clean sugar among both females and males, though with some age groups the effect is not too clear.

Cages of females were set up, in which the following combinations were compared: (*a*) one clean sugar cube; (*b*) two clean cubes; and (*c*) one clean and one fly sugar cube. While one cube may attract somewhat less than two, the total number of flies attracted to two clean cubes is generally about the same as the total attracted to one clean plus one fly sugar cube. Apparently, the total percentage attracted is not essentially modified by a low order attractant such as the "fly factor". In conclusion, the "fly factor" gives a bias to one of the two sugars, but no enhanced attractiveness to a 2-sugar combination as such.

There is no difference between the attraction of fly sugars prepared in either males' or females' cages for 15 minutes. Males respond similarly to male and to female fly sugars, as do females.

From attraction to black it was deduced that the herd instinct is more pronounced in females than in males.

Unlike *Musca domestica*, *Musca vicina*, the Levant housefly, shows no preference for the red colour.

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L'ATTRACTIVITE DES CRUCIFERES A L'EGARD DES LARVES DE *PSYLLIODES CHRYSOCEPHALA* L. (COLEOPTERE, CHRYSOMELIDAE)

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Chez les Insectes phytophages, un des aspects les moins connus des rapports Plantes-Insectes semble être le problème de la recherche de la plante-hôte par les larves néonates. Les mécanismes responsables de la découverte de l'aliment et de la prise d'alimentation sont, jusqu'à présent, relativement ignorés, tout au moins en ce qui concerne les phytophages broyeurs.

Les larves néonates de *Psylliodes chrysocephala* éclosent dans le sol au voisinage des pieds des plantes-hôtes (Chou, Colza, Navette . . .) qu'elles gagnent par leurs propres moyens. Elles pénètrent dans les pétioles de ces végétaux et y forent des galeries pendant toute la durée de la période larvaire. Les points de pénétration larvaire sont très étroitement localisés: ils sont toujours situés à la face supérieure de la base des pétioles inférieurs.

Le comportement larvaire présente trois phases successives: orientation à point de départ olfactif vers la plante-hôte et découverte d'une tige; ascension hélicoïdale mettant en oeuvre une orientation préférentielle à 45° par rapport à la direction de la lumière et à celle de la pesanteur; découverte du point de pénétration, probablement fondée sur des stimulations chimiques spécifiques de contact. Nous envisagerons ici la première phase seulement.

Le pouvoir attractif des Crucifères peut être mis en évidence soit en laissant diffuser l'odeur d'extraits liquides de broyats de plantes à l'intérieur d'une enceinte close (champ de stimulation avec gradient d'intensité); soit en utilisant un olfactomètre en Y de MacIndoo (champ de stimulation sans gradient d'intensité).

Dans un champ de stimulation présentant un gradient d'intensité les larves se dirigent vers la zone de dépôt des produits. L'analyse des trajets met en évidence: (1) des réactions d'approche: les animaux se déplacent dans la direction générale de la source de l'odeur en effectuant des trajets sinueux; (2) une forte chimiocinèse: la vitesse moyenne de déplacement des larves est environ deux fois et demie plus élevée qu'en atmosphère "inodore"; (3) des oscillations de la partie céphalo-thoracique rappelant la clinotaxie.

L'utilisation d'un olfactomètre permet de préciser l'attractivité relative des extraits de divers organes de la plante (fig. 1). Le pouvoir attractif d'extraits plus ou moins dilués de pétiole ou de tige croît avec le logarithme de la concentration relative; le pétiole se montre de 3 à 6 fois plus efficace que la tige. Des extraits de limbe foliaire sont, au contraire, répulsifs à faible concentration; pour des concentrations plus fortes l'odeur des limbes devient également attractive et son efficacité croît avec le logarithme de la concentration. Il existe probablement dans le limbe une fraction répulsive pouvant masquer l'odeur attractive quand celle-ci est très faible; le seuil d'excitation serait plus bas pour la fraction répulsive que pour la fraction attractive, mais l'efficacité de celle-ci augmenterait ensuite plus rapidement que celle du produit répulsif, en fonction de la concentration. Les extraits de racine sont inactifs.

Enfin, l'emploi de divers corps chimiques purs, testés à différentes concentrations, permet de penser que l'attractivité des Crucifères est liée, non seulement à des corps spécifiques de formule stéréochimique définie (Allylisothiocyanate), mais également à des composés assez différents (Cystéine, Acide thiomalique, 2 Mercaptoéthylamine) ou même à des corps banals (Hydrogène sulfuré); tous ces composés ayant en commun un radical sulfuré.

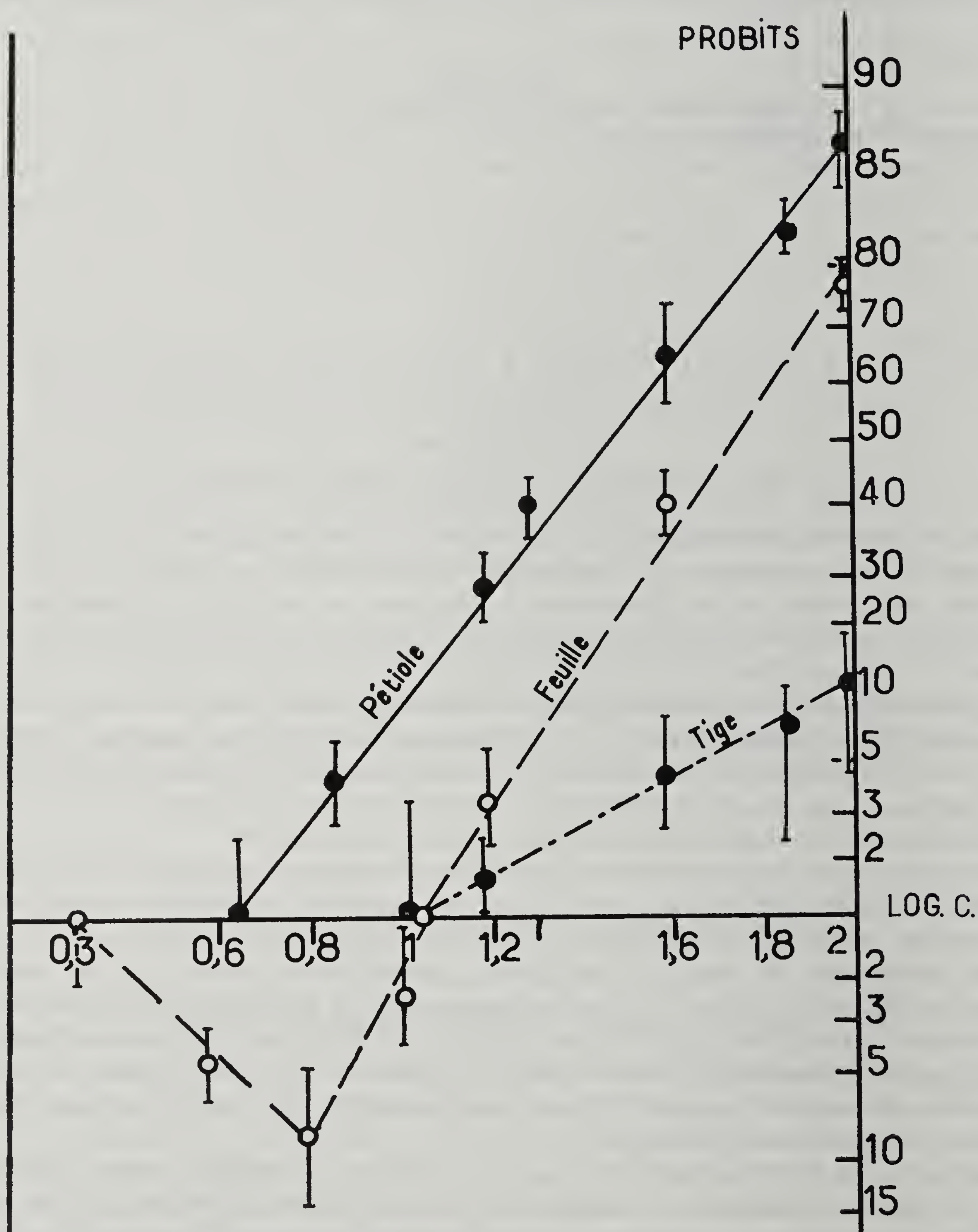

Fig. 1. Variations de l'attractivité des extraits d'organes de Chou en fonction de la concentration relative. En abscisses: logarithme de la concentration. En ordonnées: nombre de larves attirées par la solution (en probits).

COURTSHIP AND REPRODUCTIVE BEHAVIOUR

MATING BEHAVIOUR OF LOWER TERRESTRIAL ARTHROPODS FROM THE PHYLOGENETIC POINT OF VIEW

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At the transient stage from aquatic to terrestrial life, some strange patterns of reproductive behaviour have developed at several points within the animal kingdom. These differ considerably from group to group but there is a common principle which I term "indirect transference of spermatophores". The three distinctive characteristics of this are: (*a*) formation of a spermatophore, (*b*) its free deposition on the ground, (*c*) its active acceptance by the female.

This phenomenon is widespread among terrestrial arthropods of a relatively low systematic position, as follows:

1. Arachnomorpha: Scorpionida, Pedipalpida, Pseudoscorpionida, some Acari;
2. Myriapoda: Symphyla, Chilopoda, Pselaphognatha;
3. Apterygota: Collembola, Diplura, Thysanura.

With these, in the main terrestrial arthropods, there is a set scale of increasing bodily contact between the sexual partners as follows:

A. *No mating:* Males and females act in complete independence, both in space and time; e.g. Oribatei (except *Collohmannia*), Symphyla, Pselaphognatha, Collembola Arthropleona (except *Podura*);

A 1. The males add to the spermatophores a signalling device that makes search easier for the females; e.g. *Polyxenus* (Pselaphognatha).

B. *Only one mate is active:* males select sexually mature females and deposit spermatophores only when they are present; the females either
(*a*) take no notice of their "mates" (*Dicyrtomina*, Collembola Symphypleona);
or (*b*) are passively pushed to the spermatophore (*Podura*).

C. *Mating:* Two active partners are required for sperm transfer; e.g. Scorpionida, Pedipalpida, Pseudoscorpionida, Arrenuridae (water mites), *Collohmannia* (Oribatei), Chilopoda, Thysanura, *Sminthurides aquaticus* (Collembola Arthropleona).

C 1. The partners do not establish any physical contact, but "correspond" by means of chemical long-distance stimuli and "dancing acts"; e.g. *Chelifer* (Pseudoscorpionida), *Sarax*, *Admetus* (Pedipalpida).

C 2. The partners tap each other in alternating courting motions. The males secure spermic transference by means of:
(*a*) signalling webs (*Scolopendra* and *Lithobius* (Chilopoda), *Lepisma* (Thysanura));
(*b*) a filament on which the sperm is ready (*Machilis* (Thysanura)).
In addition the males of *Lithobius* signal to the females and those of *Machilis* push them to the spermic drop.

C 3. The partners grasp each other firmly:
(*a*) male holds female (Scorpionida, *Telyphonus* (Pedipalpida), *Dendrochernes* (Pseudoscorpionida), *Smithurides aquaticus*);
(*b*) male closely linked to female (Arrenuridae);
(*c*) female clings to male (*Schizonus* (Pedipalpida)).

It is typical of all the examples mentioned that, for a certain length of time, the sperm cells should be attached, outside the male or female body, to the ground or to stalks, webs or filaments. Sometimes the spermatophores do not even have special protective covers, which would seem possible only because animals employing indirect transference have continued to live in damp habitats. The ecological niche of the soil has favoured the continuance of phylogenetically old and, as it were, amphibian modes of behaviour.

The varying extension of the phenomenon of indirect spermatophoric transference and its

strongly divergent pattern within the individual groups may either rest on homology or analogy, which is a matter for speculation. It seems a safe assumption that the mating behaviours of Scorpionida, Pedipalpida and Pseudoscorpionida should be assessed uniformly from a phylogenetic angle. On the other hand, there are the astonishing parallel cases of the Collembola, Oribatei and Trombiculidae, which go a long way towards furnishing us with proof of the analogously selecting influence of the ancient common environment of the soil. This makes it evident that the soil is the oldest terrestrial living space.

Finally, with many soil dwelling arthropods, an ecological relation may be observed between living density and sexual behaviour: the greater the density the more tenuous the sexual contact pattern among the animals discussed. This is best exemplified by the mainly vegetarian Collembola and moss mites, which often congregate in thousands in a single litre of soil and for that reason alone, the females regularly encounter spermic drops by accident. Moreover, the simple structure of their spermatophores makes it possible for them to produce a large number of sperm packets in one season. The predatory arachnids and millipedes, on the other hand, whose living density is much lower, have developed effective methods of contact and communication, and the few spermatophores they produce are thus sure to be found and taken up by the females.

COURTSHIP AND MATING BEHAVIOUR IN *AGULLA* SPECIES (NEUROPTERA: RAPHIDIODEA)

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Agulla is one of the four genera in the neuropterous suborder Raphidiodea. The antiquity of this suborder (lower Permian) gives it special importance in insect evolution. The mating behavior (beginning about a week after an adult female emerges) arbitrarily has three stages: seeking, courtship, and mating. In the initial seeking the snakeflies show excited movements and prolonged cleaning of antennae and tarsi even before visual contact is made. This suggests that olfactory senses play a part in bringing pairs together. When the insects meet face to face a delicate signalling is necessary. For, in their feeding habits snakeflies will strike with a quick thrust of the prothorax and head at objects moving close to them. In courtship the male *Agulla* avoids attack by approaching slowly and at the same time rapidly vibrating his abdomen in an up and down plane. Joined with this the male has head movements (side to side and up and down), a submission of the head to the substrate and some antennal probing. The *Agulla* female's most characteristic action is a circular stretching movement of the abdomen although she may engage in actions similar to the male but less intensely. To achieve copulation the female turns to face the same direction as the male (so that the male is behind her), raises her abdomen and ovipositor and allows the male to crawl beneath her. Then the male curls his abdomen upward clasping the terminal segments of the female. Once contact takes place the female moves forward, the male loses grip of the substrate and is turned upside-down relative to the female. The two insects will remain in this position during copulation; actual union may vary from one and a half minutes to one and a half hours. A spermatophore is transferred to the female.

Comparing this behavior with information available for the genera *Raphidia* and *Inocellia* the following is noted: *Inocellia* males go beneath the female, grasp her with the mandibles, make genital contact, and maintain male beneath female position during copulation; *Agulla* males go beneath the female, make genital contact, and are then upended during copulation; finally *Raphidia* males approach the female from the side, rotate the abdoment 180 degrees in making genital contact, and then are upended during copulation. Nothing is known about the fourth genus *Erma*. It is widely considered that male beneath female is the primitive copulatory position for insects.

VARIATIONS IN THE RECEPTIVITY OF THE FEMALE *MORMONIELLA VITRIPENNIS* (Walker) (HYMENOPTERA, PTEROMALIDAE)

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Cousin (2) stated that the female *Mormoniella* (*Nasonia*) *vitripennis* will only mate once and also suggested that it ceases to be receptive, after mating, because of the presence of spermatozoa within the spermatheca. The courtship of *Mormoniella* has been described previously (1). The present paper is a further account of the female's behaviour in courtship and an investigation into the validity of Cousin's hypothesis.

Mormoniella pupae were removed from host puparia (*Musca domestica* L.) and kept separately both as pupae and as adults. There was, therefore, no possibility of contacts between individuals except during observations.

Nineteen females were kept in separate tubes and provided with honey and host pupae as food. Each female was courted by a male once only on every day of its life (=8 to 21 days). 10 females mated once only, 6 mated twice, 2 mated three times and 1 mated eight times.

The first courtship of 167 females was observed and 148 of these mated. Each of 138 mated females was observed in two further courtships immediately after the first; 45 mated a second time and 2 mated three times.

Clearly, something happens in the first courtship which affects the female's receptivity in future courtships.

After mating, the male courts the female a second time before dismounting. The female is much more likely to adopt the receptive attitude, in this post-copulatory courtship, if the male has already mated many times with other females. This result could be interpreted as supporting Cousin's hypothesis, since the male must gradually use up its sperm supply.

A female is usually receptive in its first courtship but the male can be removed, as it backs from the courtship position to the mating position, without any apparent disturbance to the female. Ten females were used, they all were receptive in the first courtship but mating was prevented. Each female was courted eight more times; two did not become receptive again, and eight were receptive in one more courtship only. The failure of these females to become receptive in courtship, even when they had not mated, is evidence against Cousin's hypothesis.

The presence of spermatozoa within the female may have a secondary influence upon receptivity. If so, this enhances a primary effect associated with courtship and the assumption of the receptive attitude.

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MEANING OF FLIGHT IN WEST AFRICAN FIREFLY, *LUCIOLA DISCICOLLIS* CAST

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The flight of *Luciola discicollis* can be classified into three categories: namely, mating-, oviposition-, and migratory flight.

In mating flight, males rise from the herbage immediately after sundown, and fly hovering over the habitat for a distance of several to 40 feet, and at a low altitude of 2-4 feet above ground, giving short, quick flashes in rapid succession with each flash lasting on average 0·34 seconds. Females in the meantime remain in the grass and flash halfway between the top and root of the grass blade: the female mating-call consists, at each flashing period, of 2-5 flashes, each for an average of 0·53 secs. There is no definite exchange of flashing between sexes, as each flashes independently of the other. Yet, there is no doubt about the sexual nature of the adult light

organs since the flashing rhythm for mating-call in both sexes differ markedly from that of creeping, flaring or migration. Moreover, when the female photogenic segment was coated, males failed to find her except by an accidental body contact.

The oviposition flight is so named because females are unable to lay eggs without flight. The flight is marked by a very low altitude of 1-2 feet and by a short distance of a few feet only. It was found that when the females were confined within a small container in which they could not fly, no oviposition took place, while when the insects were placed in a larger container which is at least 1 × 2 × 1 feet in which they could flit, eggs were normally laid as in nature. Dissection of the females in the small container showed that the vitellaria contained fully mature eggs but none were in the ovarial sacs where the eggs are stored prior to oviposition. Consequently, the oviposition flight is of prime importance for egg-laying, since it helps mature ova to descend from vitellaria to ovarial sacs.

The migratory flight takes place on calm, dark, and humid evenings from after-sunset to about 8 p.m. The insects fly from 7-40 feet (usually 20-30 feet) high and may cover a distance of a few thousand feet. The migrants are all sexually mature females which rise from their home site individually and independently of each other with the speed of 3-5 miles per hour. The flashing rhythm is averaged 0·75 secs. per flash at the height of 7-20 feet; 1·2 secs. over 30 feet. The migrating females are answered by a number of males on the ground which brightly flare on top of vegetation, each flare lasting from 2 to 6 secs, averaging 3·6 secs, so that the migrants may land in the new area inhabited by their own species. The new-comers may mate in the new habitat and at least a part of their eggs are laid there. Since the larvae were found to feed on the firefly eggs in a densely populated condition, it is probable that when the larval population exceeds a certain limit, some of the females in the area migrate into less crowded areas for oviposition. Probably the females recognise the larval population by their lights. At any rate, the migration of fireflies contributes both to the survival of the species and gene flow.

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INFLUENCE DE LA PERIODICITE LUNAIRE SUR L'ACTIVITE DE QUELQUES NEMATOCERES HEMATOPHAGES

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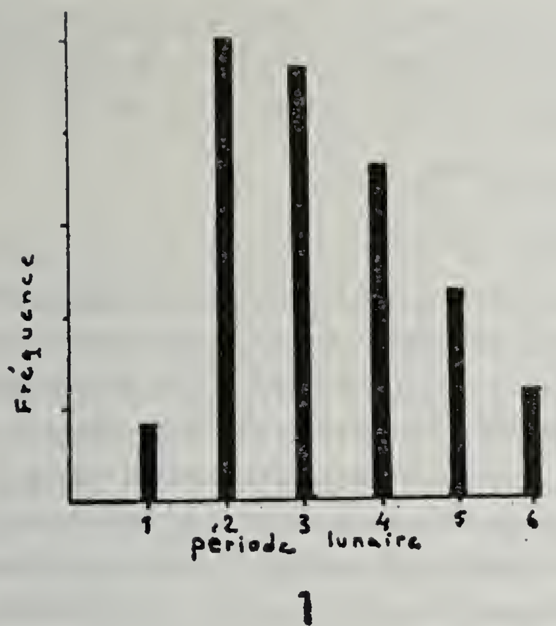
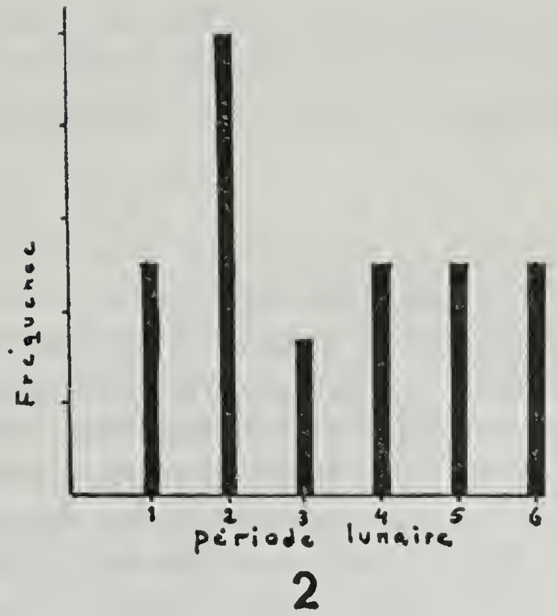
L'auteur a trouvé une relation entre le nombre d'individus capturés par moyen d'une piège à lampe et le cycle lunaire, pour beaucoup d'espèces de Nématocères hématophages. Pour analyser ce phénomène, le mois lunaire fut divisé en six périodes. La première période dans laquelle est située la pleine lune, contient 4 ou 5 jours; les autres périodes contiennent toujours 5 jours. Quelques exemples de ce phénomène: les nombres corrigés d'*Alluaudomyia sordidipennis* ♀ trouvés pour chaque période sont respectivement: 5·5 - 2·5 - 0·3 - 0·5 - 2·0 - 3·8, n = 27; *Atrichopogon distinctus* ♂: 18·0 - 25·5 - 18·5 - 28·8 - 22·1 - 46·5, n = 285; *Culicoides ochrothorax* ♀: 14·0 - 44·5 - 105·8 - 147·7 - 61·5 - 29·2, n = 834; *Forcipomyia fuliginosa* ♀: 94·5 59·8 - 50·7 - 67·5 - 88·2 - 116·5, n = 867; *Anopheles nili* ♀: 1·0 - 0 - 2·7 - 9·2 - 10·0 - 4·5, n = 63.

La même connexion entre phase lunaire et nombre d'insectes capturés fut trouvé pour les Culicidés attrapés pendant le jour (5·30-7 h. et 16-18 h.) par trois capteurs dans des endroits déterminés. Exemples: *Anopheles paludis* ♀: 7·5 - 8·4 - 13·8 - 16·9 - 11·0 - 12·3, n = 125; ♂: 1·6 - 1·9 - 4·3 - 6·8 - 2·9 - 6·2, n = 38; *Mansonia uniformis* ♀: 425·1 - 397·1 - 417·3 - 411·2 - 607·0 - 634·8, n = 4,928; *Culex tigripes* ♀: 27·8 - 28·9 - 54·1 - 26·2 - 31·8 - 22·4, n = 284; ♂: 9·5 - 5·8 - 15·3 - 7·9 - 7·5 - 5·1, n = 72. Les graphiques des lampes et ceux des capteurs sont suffisamment conformes. Pour expliquer ce phénomène on peut penser à deux possibilités:

1. l'éclosion simultanée des pupes,





FIGS. 1, 2. Influence lunaire sur l'activité de quelques Nématocères hématophages.

2. une activité intensifiée des adultes sous l'influence de la lune.

Dans le premier cas on doit s'attendre à un graphique qui montre soudainement un nombre très élevé, suivi par une diminuation graduelle par suite de la mortalité normale (fig. 1). Il semble que ce n'est pas le cas.

En outre il n'est pas probable que les larves se développant dans des gîtes tellement dépendants de facteurs climatologiques comme des marais peu profonds, des boîtes de conserves etc., auraient fini leur cycle toujours dans le même temps.

Il nous reste donc à considérer une activité intensifiée des adultes. Dans ce cas on peut s'attendre à un graphique comme dans la figure 2, dans laquelle le nombre d'individus est à peu près égal pendant toutes les périodes pour n'augmenter que pendant la période de l'activité intensifiée. Ce graphique théorique s'accorde assez bien avec les chiffres trouvés. Cette activité peut être causée soit par une tendance à migrer, soit par un comportement sexuel different, soit encore par les deux facteurs agissant simultanément. Si l'on compare les graphiques des animaux capturés chez les gîtes larvaires avec ceux attrapés ailleurs, on constate que plus on s'éloigne des gites, plus le maximum se trouve retardé. Ce fait ne se laisse pas expliquer seulement par l'activité sexuelle, mais s'accorde bien avec la migration.

Quelques années d'observations sont encore nécessaires pour confirmer les faits mentionnés ci-dessus.

A PHOTOGRAPHIC ANALYSIS OF MOTH FLIGHT BEHAVIOR WITH SPECIAL REFERENCE TO THE THEORY FOR ELECTROMAGNETIC RADIATION AS AN ATTRACTIVE FORCE BETWEEN THE SEXES AND TO HOST PLANTS.

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Callahan (1) postulated an electromagnetic theory of host plant finding and communication between sexes of moths. Laithwaite (2) postulated a similar theory for attraction between the sexes. A photoelectric-photographic analysis of moth flight showed several species of Noctuidae, Arctiidae, and Sphingidae responding to extremely low light intensities with antennae, proboscis, and oviposition responses. As there was no scent present, it was felt that the response was to some portion of the electromagnetic spectrum and not to scent molecules. The corn earworm (*Heliothis zea* (Boddie)), is capable of raising its thoracic temperature 8°F above the ambient and the Abbot's sphinx (*Lapara coniferarum* (A. & S.)), 17·8°F above ambient. The far infra-red output of the thermal parameter of these moths was shown to be in the 8 μ to 10 μ FIR region. The corn earworm flies at periods in nature when FIR transmission would be at its maximum efficiency. Moth flight and oviposition was shown to be reduced during full moon when 8 μ to 14 μ emission from moon would be expected to interfere with the behavior of moths dependent upon an FIR parameter. The configurations of the four main types of spine on the antennae of the corn earworm, when treated as resonant cavities, could be expected to tune to an E_0 resonant mode at frequencies of 34·8 mega-megacycles, 50 mega-megacycles, 125 mega-megacycles, and 250 mega-megacycles (8·6 μ, 6·0 μ, 2·35 μ, and 1·17 μ, respectively. Such a range of intermediate and far infra-red thermal resonant configurations would cover the identification of total moth radiation, host plant radiation, and radiation from molecules of sex identification substance (releasers). Wright's (1963) theory of identification of sex substance molecules by infra-red frequencies would appear to be entirely correct.

The night-adapted eye of the corn earworm moth has the correct configuration for an infra-red mosaic optic-electromagnetic thermal radiometer and could thus be a night FIR radar unit capable of spotting "hot" points of FIR radiation against cool night backgrounds. This hypothesis is based on the fast daylight adaptation response of the eye to ultraviolet light (3654Å) and the fact that at night crystalline cone, with the configuration of a field lens, is coated by a pigment which is a quarter wave of the calculated corn earworm FIR emission in the 8·6 μ to 10 μ band. To operate in the IIR or FIR, it would be necessary for a field lens to be coated with a quarter wave anti-reflection dielectric. All morphological units, including those of the corneal lens and rhabdom (detector), fit the theoretical configuration to be expected of a mosaic optic-electromagnetic thermal radiometer.

Various species of Noctuidae, Arctiidae, and Sphingidae moths and larvae were subjected to high intensity intermediate and far infra-red frequencies in the 1 μ to 30 μ band and to silver chloride filtered low intensity intermediate and far infra-red frequencies in the 3 μ to 30 μ band. High intensity infra-red focused into the eye killed moths in an average of 60 sec at a thermal parameter of 120°F. Low intensity infra-red focused on the antennae or eye elicited various flight, antennal, and sexual responses at thermal parameters of 85°F to 92°F. Low intensity infra-red at a thermal parameter of 92°F focused on the ocelli of larvae elicited fecal pellet deposition and searching and head scanning of larvae. The various reactions are substantially in agreement with Callahan's theories that the antennal spines are infra-red resonant cavities, the night-adapted eyes are mosaic optic-electromagnetic thermal radiometers, and the ocelli are immersed detectors for infra-red location of host plants.

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FOOD RESERVES IN THE REPRODUCTIVE CASTES OF *LASIUS FLAVUS* FAB. (HYMENOPTERA)

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The carbohydrates ("glycogen") in individual queens and groups of five males were estimated with the anthrone reagent by the indirect method of Seifter *et al.* (4). Lipid content was obtained by extracting groups of five queens or fifty males to constant weight, after drying, with petroleum ether.

Males and queens were collected as they emerged from the nest for the nuptial flight and analysed. Queens were also analysed after fertilisation and after producing an average of one worker per queen when allowed to found a colony singly and in groups of five and ten.

3·77% of the wet weight of the queens was "glycogen" before the nuptial flight and slightly less (3·71%) afterwards. The males, in contrast, contained large quantities, 7·37% of their wet weight.

After colony foundation, the queens were found, on the average, to contain a much smaller amount of glycogen, ranging from 5% down to negligible quantities. As far as the small samples allowed it was concluded that there was no relation between the amount of glycogen and the size of the group co-operating in founding the colony.

The fat reserves of the queens were substantial, forming 37·78% of the wet weight and 62·39% of the dry, when they emerged from the nest. Even after colony foundation the fat represented a large proportion of the body weight. In queens that had reared broods in isolation 13·69% of the wet weight and 40% of the dry weight was fat. In those which had co-operated in groups of five and ten the figures were 28-29% and 56% respectively, there being little difference between the two groups. If these proportions are related to the original weight then, in the isolated queens, fat represents 13% of the original dry weight, that is four fifths have been lost. In the grouped queens the remaining fat represents 40% of the original dry weight, therefore only one third has been used.

The males were again remarkable, because of the minute amounts of fat they contained, 7·73% of the dry weight and 2·74% of the wet weight.

When compared with other insects (1, 6 and 7) the quantity of glycogen found in the queens, both on the average and from individual to individual was quite large but not outstandingly so. The glycogen content of the males, in contrast, was only exceeded by some insect larvae (7) and was greatly in excess of figures quoted for adults.

The average fat reserves of the queens were much greater than those found elsewhere in the insects, though the individual variations could be matched by migrating Lepidoptera (2 and 5). Equally, the amounts found in the males were more in keeping with exhausted, migrating insects (2, 3 and 5).

The small amounts used by the queens in what must be assumed to be optimum conditions for colony foundation (i.e. in groups of 5-10) re-emphasise the importance of other sources of nutrition utilised by these insects during their prolonged fast.

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NOTES ON OBSERVATIONS OF THE BEHAVIOUR OF A SOCIAL WASP *POLISTES HEBRAEUS* (HYMENOPTERA)

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A large comb was found (23.9.62) of *Polistes hebraeus* Sauss. (Vespidae) at Pilani (Rajasthan), India, on a dead branch of a *Casuarina* tree, wherefrom it was removed to a *Prosopis* tree. All observations were made in this new site till the cessation of the colony (25.11.62).

Foraging. Foraging takes place only in the day time and is largely regulated by the prevailing temperature, which is important because in the colder season the time of foraging becomes progressively shorter. 71°F appears to be minimum temperature for foraging at this time of the season and at no time more than 1/6th of the total population of the comb was out foraging. Cloudiness of the sky is a deterrent to foraging.

Behaviour of the individual. Individual wasps were caught and marked. Foraging is done only by workers, each taking about 3-7 minutes per excursion. One worker made 3 trips within 15 minutes but none in the subsequent 40 minutes when the sun was behind cloud. Workers seem to feed the grubs directly although they feed the queens and the males as well.

Mating behaviour. Although comb-building starts in March or early April, sexual forms do not appear until October. Males are somewhat bigger than workers and have squarish heads; abdomens of the females are perceptibly bigger than those of workers, but there is intergrading. Mating takes place soon after emergence and, unlike bees, on the comb itself. I believe these wasps practise both polyandry and polygamy. The sexual forms do not forage but are fed by the workers.

Hovering activity and swarming. After the mating season, sexual forms are driven from the comb. Males repeatedly try to come back but are driven off by the workers. At this part of the season (late autumn) there is much hovering activity near the comb and also males are found among the flying wasps. Both males and fertilised females frequently enter houses in large numbers to hibernate. This large scale departure of the sexual forms from the comb may be called *swarming* or exodus of the sexual forms.

Sun-compass and memory. Flight is largely dependent upon visibility of the sun. Flight activity is considerably reduced when the sun is covered and *vice-versa.* The wasps show a considerable memory and many continued to return to the old nest site for more than a day after the site had been changed.

Behaviour in cold weather and extraction of sting poison. At temperatures below 55°F they are unable to fly and sit with their wings at 45° to the body, and on disturbance do not take to flight. In this condition they may be picked up with forceps and the tips of the abdomina touched with a microscope slide. This causes immediate thrusting out of the sting with a drop of poison which may be collected. The B pH ranges from 5·9 to 6·4.

Hibernation. Females at Pilani hibernate from the beginning of December until the end of February. Males also attempt to hibernate but soon disappear. On December 9th female wasps found behind calendars in my house were marked and left there. All except 2 stayed there till the end of February and then flew away. On 3.3.63 I found some wasps flying about in my house, one of which had been marked.

The comb. Normally the comb is circular with only a single tier. This comb was 8·5″ in diameter with a total of 1,192 cells. Cells containing sexual forms are taller than the rest and usually placed near the periphery.

LOCI OF SENSORY END-ORGANS USED BY COCKROACHES IN MATING BEHAVIOR

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Olfactory and tactile stimuli are principally responsible for releasing various patterns of behavior during courtship and mating in both sexes of most species of cockroaches.

By means of ablation, a study was made of the relative importance of the antennae, mouthparts, and cerci, in mating behavior of *Nauphoeta cinerea* (Olivier), *Leucophaea maderae* (Fabricius), *Byrsotria fumigata* (Guérin), and the bisexual strain of *Pycnoscelus surinamensis* (Linnaeus).

In *N. cinerea*, *L. maderae*, and *B. fumigata*, female sexual behavior (mounting and feeding on the male's terga) is released by a male pheromone. The female's antennae serve as distance chemoreceptors for perceiving male odor and her ability to mate can be correlated with distribution of thin-walled chemoreceptive types of sensilla on the antennae. The mounting and feeding response of *N. cinerea* females released by extracted male pheromone also was correlated with distribution of chemoreceptive sensilla on the antennae. Apparently, in *B. fumigata* females only the antennae perceive male stimuli. However, in *N. cinerea* and *L. maderae*, sensilla on the last segments of the maxillary and labial palps also are capable of detecting the male. However, the palpal sense organs do not serve as efficient distance receptors, even though these distances are short. *P. surinamensis* is unique in that headless females are capable of mating; this may be explained by the fact that these females do not feed on the male's terga prior to copulation.

The behavior of males of *N. cinerea*, *L. maderae*, and *B. fumigata*, after ablation of various sense organs, differs from that of the females in that it was impossible to eliminate mating. The antennae bear the receptors for effecting a rapid response to females. However, the maxillary and labial palps, and cerci (except in *B. fumigata*) also play a role; the importance of these organs is shown only by combined removal with the antennae. The difficulty in eliminating mating in males of *N. cinerea* and *L. maderae* probably reflects the ease with which they show courtship behavior apparently by tactile stimulation alone, in the absence of females. However, *B. fumigata* males rarely court in the absence of females and it is probable that after antennectomy, palpectomy, and cercectomy, other sense organs (e.g. on the mouthparts other than palps) can detect female pheromone.

The antennae of *P. surinamensis* males serve as distance receptors for sex odor. The male's response to the female's pheromone can be correlated with receptors on antennal segments 9 and beyond. After antennectomy, sense organs on the last segment of the maxillary palps of the male can detect the female on contact.

CONTRIBUTED PAPERS

OBSERVATIONS ON *ZONOCERUS VARIEGATUS* (LINN.) (ORTHOPTERA) IN SIERRA LEONE

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Zonocerus variegatus is a Pyrgomorph grasshopper widespread in West Africa. It has one generation a year wherever it occurs, but the life history is related to rainfall, and populations in different places are out of step. In wet regions the eggs hatch after the last rain of the season, and nymphal development and adult life go on during the dry season, the adults dying before the next rains. There are six nymphal instars in both sexes, the total duration of which is about 3-4 months. Wing reversal occurs at the fifth instar.

Some nymphs were kept in cages under "crowded" conditions; about 200 in a cage of 250 litres or 50 in cages of 57 litres. They were not crowded as densely as is necessary to produce phase *gregaria* in locusts. Crowding had a marked effect on the rate of development; crowded females completed the sixth instar in 13·5 days while solitaries took 15·7 days. For males the times were 14·2 and 15·6 days. The differences are significant in both sexes. The mean weights in milligrams of newly-emerged adults were: females, crowded, 914, solitary, 1165; males, crowded 993, solitary 1009. The differences between the sexes were significant, and solitary females were significantly heavier than crowded.

There were no morphological differences between solitary and crowded individuals, and this suggests that in the evolution of gregarisation physiological changes preceded structural ones.

Response of nymphs to light

First and second instar nymphs congregate on the tops of bushes at sunset and sunrise, where the light intensity is about 5,000 lux. In cages, they arranged themselves in a circle round a central lamp in the roof, where the light intensity was about 5,000 lux.

Older nymphs were exposed to light the intensity of which was varied by altering the applied voltage. The proportion responding was lower than in young nymphs, but sufficient to show that, while a decrease in intensity resulted in movement toward the lamp and an increase in movement away, the movements were not sufficient to bring the insects into the same light intensity as that they had just experienced. The number responding was greater with a falling light intensity than with a rising one.

The advantage to young nymphs of aggregating and keeping together may be that they are better protected by their disagreeable odour.

Adult male *Z. variegatus* produce a low-pitched buzz, lasting about one second, when they are approached by another male. The approaching male sometimes moves away, but may mount the buzzing male. The sound is still produced after the wings, elytra and hind legs have been removed. The occlusion of the thoracic and first and second abdominal spiracles greatly reduced the volume of sound. The corner of the pronotum was cut off, exposing the air sac at the base of the first leg. Buzzing was accompanied by a swelling of this air sac, and a backward movement of the pronotum.

DISPERSION BEHAVIOUR OF ADULT BEETLES IN GRAIN

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Over the past five years attention has been directed to a study of the distribution of insects in laboratory-scale bulks of grain. The primary aim of these studies has been to assess the influence of physical factors on individual movement, dispersal and group formation. The species used were *Tribolium castaneum* (Hbst.), *Sitophilus granarius* (L.), *Oryzaephilus surinamensis* (L.), *Cryptolestes ferrugineus* (Steph.) and *Rhyzopertha dominica* (Fab.).

Dispersion, which is defined as the spatial structure of a population, had typical specific characters and varied with physical conditions. A basic feature of individual behaviour is random movement throughout the grain. In groups this causes mutual disturbance which elicits negative geotaxis, the disturbance factor being related to individual weight and rate of movement. Thus the numbers on the surface of grain samples and the patterns of vertical dispersion vary with the intensity of movement. Accumulation occurs in restricted loci where kinesis is minimal although the mechanism of response to the particular physical conditions may be either orthokinetic or klinokinetic.

As a result of experimental studies on the spatial structure and organisation of these populations, the following hypothesis is being developed. Random movement is considered to be a fundamental component of dispersion behaviour, certainly in insects. Modification of this intrinsic pattern of individual behaviour by external stimuli, mediated by way of the organism's sensory-motor apparatus, results in the spatial structure of populations within an environmental complex. A relatively uniform spatial structure, may represent a dynamic equilibrium of the population within natural or physiological-behavioural boundaries due to differential kinetic levels which are the result of environmental heterogeneity. The spatial structure is of survival value to the population. The study of random movement and its modification by response to environmental stimuli provides a unifying principle in the study of dispersion behaviour and the analysis of eco-ethological systems. Mutual interaction in populations arising from individual movement giving rise to the generalised *disturbance* → *dispersal* → *dispersion* sequence of events, can form the basis of primitive territorial and social behaviour. Within the spatial organisation of a population, intrinsically controlled by individual behaviour, the various processes of population metabolism and dynamics can take place.

L'EFFET DE QUELQUES FACTEURS SUR LE DEVELOPPEMENT DU NID A COUVAIN DE L'ABEILLE (*APIS MELLIFERA* L.)

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L'effet des facteurs suivants sur le développement du nid à couvain a été examiné pendant la saison active.

1. *La température extérieure—Capacité de la colonie—Isolation de la ruche.*
   Le développement du couvain ne peut être empêché en été par l'instauration artificielle d'une basse température ambiante, qui correspond à la température automnale par laquelle l'activité d'élevage est arrêtée. Le développement du couvain se révèle donc en grande partie indépendant de la température extérieure.
2. *L'Humidité de l'air*
   L'expérience laise supposer que le développement du nid à couvain peut être influé par l'humidité de l'air, ce qui toutefois devrait être soumis à un examen plus approfondi.
3. *L'activité des butineuses—Plantes nectarifères—Sources d'eau disponibles*
   Il parait y avoir une concordance frappante entre le vol total des abeilles et le développement du nid à couvain.

TIME LAPSE PHOTOGRAPHY AND HUMIDITY GRADIENT EXPERIMENTS

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In many humidity behaviour studies, periodic observations on the positions of animals in alternative chamber and ring/channel gradients are made during relatively short periods such as a quarter to one or two hours. Such records indicate those zones in which aggregation occurred and upon which the nature of the humidity behaviour is evaluated. It is believed that such zones of aggregations may represent temporary responses as has been found in a number of species. Furthermore, the lack of standardisation of the animals prior to testing by some form of pretreatment, which not only induces a more uniform response but also permits correlation with the precise physiological condition of the animals, makes an appraisal of such responses difficult.

Because of the need to observe, for relative long periods in humidity gradients, animals which had been standardised by some form of pretreatment, time lapse photography was considered. The use of time lapse photography in gradient studies does not appear to have been employed hitherto although it has been used in other types of behaviour study.

The photographic apparatus consisted of an automatic recording camera coupled to an intervalometer and electrical control box so that it could be operated at preset intervals from a mains supply. The electronic flash was synchronised to the camera and was 0·001 sec. in duration, power for which was obtained from a power pack connected into mains supply. Each was supported by a specially designed stand giving maximum manoeuvreability.

Although the literature suggested that electronic flash had no obvious effect upon the behaviour of *Aedes*, this was not found to be the case with the stored product beetles, *Carpophilus dimidiatus* and *C. hemipterus* where activity was used as the criterion of response. It was found that both a high rate of flashing and a high flash illumination induced a higher activity level in the former species whereas only the rate of flashing was of consequence in the latter. However, in both cases conditions of minimal response were established and these were considered sufficiently minor to allow the technique to be used to assess its suitability with respect to gradient studies.

The behaviour of standardised *C. dimidiatus* in a perspex channel apparatus containing a monofacial humidity gradient (20%–80% R.H.) was recorded using time lapse photography for 12 hours in each of four days at 25°C. Examination of film negatives revealed that the technique had been successful in recording positions of the animals and was subsequently confirmed for other species.

Time lapse photography not only overcame the difficulties associated with direct visual observations but also provided a permanent record from which further examination could be undertaken. Furthermore, facets of the behaviour may be indicated which would not have come to light with other techniques. A disadvantage of the photographic technique is that faults in the setting of the camera, its accessories and the film processing could jeopardise the study but experience should minimise these difficulties.

Time lapse photography has an invaluable role in humidity gradient studies and its appreciation will undoubtedly result in a more comprehensive evaluation of animal behaviour.

POSSIBLE HYGRORECEPTORS IN THE BED BUG *CIMEX LECTULARIUS* L.

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Studies carried out in an alternative chamber on the reactions of the bed bug *Cimex lectularius* L. towards humidity have clearly demonstrated that it is a hygronegative insect. A range of indifference was shown to extend between 18 and 50% R.H., outside which all humidities are avoided. The striking avoidance of the moist side shown by the insect at 30

and 75% R.H. was made use of in an attempt to locate the humidity receptors. The antennae, being the seat of a number of sense organs as reported by several authors were tested in a series of experiments. When both antennae were amputated, the disappearance of the humidity response soon became obvious and the operated individuals were indifferent on crossing from the dry to the moist side of the arena. Having obtained this result repeatedly, amputation of the antennae at different levels was then performed to locate the probable site of humidity perception. It was found that the bed bug was able to respond to the humidity difference offered and avoided the moister side when either the fourth (apical) segment in the two antennae or both the third and fourth segments were extirpated. On the other hand the humidity response was entirely eliminated when amputation included the second antennal segment (Table I). The same result was obtained when just the distal half of this segment (together with the third and fourth segments) were bilaterally removed or covered with cellulose paint. This area was then carefully examined, and it was found to contain 4-6 minute tuft organs, each arising from a saucer-shaped depression and innervated by a group of bipolar cells.

TABLE I

Intensity of reaction of *Cimex lectularius* L. towards the alternative 30-75% R.H. when the antennae are amputated at different levels

Exp.	*No. used*	*Bilateral amputated segments*	*Intensity of reaction* *min.*	*Bilateral amputated* *max.*	*average*
1	15	4*th* (apicals)	43	51	47
2	15	4*th* + 3*rd*	38	47	45·5
3	15	4*th* + 3*rd* + 2*nd*	0	0	0
4	15	4*th* + 3*rd* + distal half of 2*nd*	0	0	0
5	15	intact	40	53	49

This disappearance of the response of the insect to humidity when the distal half of the second antennal segment on either side is covered or extirpated, and its appearance again when this part is intact suggest that the tufted sense organs may be sensitive to humidity and may function hygroscopically (1). This was supported by results obtained from experimental studies on the hygrometry of the dead cuticle (cast skin) of the bed bug which clearly indicated that it is highly hygroscopic; its weight being more sensitive to humidity changes in the upper part of the humidity scale. To this may be added that the insect has often been observed on encountering the moist half of the arena to swing its antennae at the humidity boundary and soon recoil to the drier half.

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FACULTATIVE VIVIPARITY IN *MACROCHELIDAE* (ACARI: MESOSTIGMATA)

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It has been proved that a fimicolous macrochelid mite, *Macrocheles peniculatus* Berl. can lay eggs or larvae according to ecological conditions. Twelve species of macrochelids have been successively tested for oviparity-viviparity under the influence of 8 standard treatments in order to study the comparative behaviour of various species.

The macrochelids investigated belong to 3 genera, (1) *Areolaspis, A. sp.*, (2) *Glyptholaspis, G. americana* (Berl.) and *G. confusa* (Foà), and (3) *Macrocheles, M. merdarius* (Berl.) *M. muscaedomesticae* (Scopoli), *M. penicilliger* (Berl.), *M. peniculatus* Berl., *M. perglaber* Filipponi e Pegazzano, *M. robustulus* (Berl.), *M. sp.*, *M. subbadius* (Berl.) and *M. vernalis* (Berl.). They are all dung-living mites; two of them, *M. penicilliger* and *M. peniculatus*, being thelytokous, the others arrhenotokous.

The 8 treatments rise from the combinations of two levels for each of the three following factors (1) food: F_1, frozen house-fly eggs and living nematodes on ground steer manure as substratum, and F_2, substratum only; (2) aeration: A_1, good aeration through a 2 cm. hole and A_2 poor aeration through a pinhole; (3) treatment duration: D_1, 2 days period and D_2, 4 days period. Four groups of 30 females have been allowed to lay progeny in tubes, immediately after treatments on little amounts of substratum, with food, for 3 hours period, after which laid eggs and/or larvae have been counted. Factorial analysis has been carried out on angular transformations of the percentages of the females which laid eggs and those which laid larvae. All 12 species have been shown to be facultatively viviparous.

Feeding appears to be the factor with the greatest influence on the mode of reproduction, plentiful food favouring oviparity in any case, fasting viviparity. The influence of the other two factors and of ecological conditions determined in the substratum by the different combinations of their modalities seems to be more limited and affects the various species in different degrees and, sometimes, with opposite results. As a consequence, the relative frequency of viviparity for all of the 8 treatments varies according to the species, ranging from 0·96 in *M. merdarius* to 0·17 in *M. penicilliger*. The extreme ends of this range are very near to exclusive oviparity or exclusive viviparity, the more generalised conditions, which would be present also in macrochelids.

Females of *M. muscaedomesticae* and of *M. peniculatus* have been also tested for facultative viviparity just after a controlled period of phoresy, on *Musca domestica* L. and on *Bubas bison* L. respectively, and they have laid larvae only, as after fasting treatments.

The most important of the stimuli for oviposition seems to originate from the pressure exerted by the explosive growth of the oocyte which immediately follows the arrival of the mature egg in the uterus. This explains the prevalent influence of feeding, common to all species. Another stimulus could originate from the agitation of the hatched larva in the uterus, the response to which varies in the different species.

The adaptive value of the phenomenon of viviparity or oviparity in fimicolous macrochelids is emphasised.

ETUDE DE LA REPARTITION DES LARVES NEONATES D'*ACANTHOSCELIDES OBTECTUS* SAY

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La distribution d'*Acanthoscelides obtectus* dans les stocks est liée exclusivement au comportement des individus des deux stades susceptibles de se déplacer à l'extérieur des grains: adultes et larves néonates. Les déplacements des adultes conduisent à une distribution déterminée des pontes à l'intérieur du stock. Mais la répartition des insectes dans les grains dépendra en définitive des déplacements des larves néonates. Cette densité larvaire dans les grains influence considérablement le poids et la fécondité des adultes et ainsi l'évolution numérique de la population.

Nous avons montré (1) que lors de leur pénétration dans les grains, plusieurs larves avaient tendance à utiliser le même orifice. Un tel comportement concentre les larves dans un nombre limité de grains appartenant à un groupe de grains contigus. Cette concentration implique que les larves se trouvent préalablement rassemblées au niveau de grains très voisins.

Ce groupement peut évidemment résulter de l'émission par les femelles de paquets comprenant plus de 20 oeufs. Cependant l'importance des déplacements des larves néonates (2) est telle qu'ils peuvent éventuellement influer sur la distribution des individus dans les grains.

Pour contrôler cette action nous avons examiné l'influence de la répartition des grains sur la position définitive des larves. Nos résultats résument de nombreuses expériences effectuées, à l'obscurité constante, en boîtes circulaires de polystyrène de 220 mm de diamètre. Les lots d'oeufs étaient déposés au centre dans une capsule de 10 mm de diamètre.

Lorsque les grains sont à 80 mm des oeufs, il n'y a pas augmentation de la mortalité larvaire.

Quand des séries de 5 grains, en contact les uns avec les autres, forment 4 lignes partant de la capsule contenant les oeufs, *la répartition est fonction de la distance des grains.* Lorsque les ouvertures de la capsule ne corrèspondent pas aux lignes, le nombre de larves par grains diminue régulièrement de moitié (r = 1/2) en fonction de la distance des grains ($\chi^2 = 2{,}43$ pour 4 D.L.)

Tableau I

Répartition des larves *d'Acanthoscelides obtectus* dans 4 séries de 5 grains partant de l'emplacement des oeufs

effectif d'oeufs	*nombre de répétitions*	*effectif bruches*	*1er grain*	*2ème grain*	*3ème grain*	*4ème grain*	*5ème grain*	
50	8	*observé*	164	62	41	32	10	$\chi^2 = 11{,}46$
		théorique $r = \frac{1}{2}$	159,5	78	40	20	10	
100	8	*observé*	237	117	122	79	26	$\chi^2 = 100{,}9$
		théorique $r = \frac{1}{2}$	300	150	75	37,5	19	

Par contre, lorsque les ouvertures de la capsule sont en face des lignes, la distribution dépend de l'effectif initial (tableau 1) et présente une différence significative avec la répartition exponentielle du cas précédent. Il y a tendance à l'uniformisation de l'effectif des larves, indépendamment de la distance des grains. Ce phénomène est particulièrement net quand les effectifs initiaux sont de 100 oeufs.

Cette modification de la distribution provient d'une *compétition avant la pénétration* car, pour les premiers grains, avec un effectif initial de 100 oeufs, le nombre d'individus par grain varie de 0 à 25, soit un peuplement toujours relativement faible.

L'attraction exercée par les grains est faible. Car, en présence de 2 couronnes de grains, la première discontinue à 40 mm de la position initiale des oeufs et occupant effectivement un tiers de la circonférence, la seconde continue à 80 mm, l'effectif de bruches issu des grains de la première correspond à 39% du total.

Lorsqu'il y 9 paquets de 3 grains à 65 mm des oeufs, la distribution à l'intérieur des paquets est hétérogène, sans que la position de certains grains soit systématiquement priviligiée. La distribution entre les différents paquets est aussi hétérogène, de même que la distribution entre les secteurs formés par 3 paquets voisins. Mais ceci ne correspond à aucun gradient lié à une hypothétique polarité à l'intérieur de l'étuve.

Lorsque les grains sont à plus de 60 mm des oeufs, quel que soit leur type de répartition, toutes les analyses montrent une grande hétérogénéité dans la distribution, impliquant: soit un déplacement plus ou moins groupé des larves, soit l'utilisation des mêmes parcours par plusieurs larves.

Les déplacements larvaires concourent à rassembler les larves avant la pénétration et à provoquer une concentration anormale d'individus dans certains grains.

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COMMUNICATION BETWEEN INSECTS

PHYSIOLOGIE DE L'ATTRACTION SEXUELLE CHEZ *BOMBYX MORI* L.

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Chez les Lépidoptères le rapprochement des sexes est basé sur l'olfaction.

L'organe de l'attraction porté par la femelle est un repli épithélial glandulaire de l'ovipositeur qui émet une substance chimique excitant des récepteurs situés chez les mâles sur les antennes.

Cette substance a été extraite d'abdomens de *Bombyx mori* ♀ par Butenandt et sa formule chimique établie (2, 4 Hexanedienol).

L'étude physiologique entreprise par nous depuis 4 ans a mis en évidence les faits suivant chez *B. mori*.

L'attraction s'accompagne, du coté ♀ comme du coté ♂ lors de la réception, d'attitudes se succédant dans un ordre à peu près constant et qui, bien notées, ont permis d'apprécier le seuil d'action de l'émission odorante et de comprendre diverses expériences.

La puissance attractive des ♀ et des bourrelets glandulaires isolés, a été mesurée par la distance maximum à laquelle un ♂ neuf réagit.

Les glandes formées avant la mue nymphale et déjà chargées de substance, n'attirent que lorsqu'elles sont protrusées, après expansion et séchage des ailes, 1/2 heure environ après la fin de la mue imaginale; elles atteignent alors, en moins d'une heure, leur puissance maximum, puissance qu'elles conservent à chaque protrusion jusqu'à l'approche de la mort où elle diminue rapidement.

Chez les ♀ entières, même isolées des ♂, la protrusion n'est pas continue: normalement, elle cesse pendant l'accouplement et la ponte, ce qui est logique pour un appareil destiné à favoriser la conservation de l'espèce, mais elle reprend après la ponte ou les pontes successives et même en l'absence d'ovules à émettre, ce qui est surprenant.

Cette alternance: protrusion-ponte est due surtout aux dispositions anatomiques: La ♀ ne peut, en même temps, extroverser le bourrelet pour émettre l'attractif et étirer son ovipositeur pour déposer les oeufs. L'excision expérimentale prive l'ovipositeur de la longueur que lui donne l'effacement du repli, et l'empêche de déposer convenablement les oeufs.

Relation fonctionnelle avec l'appareil reproducteur: La castration, voire l'ablation peu de temps avant la chrysalidation, des ébauches de tout le tractus (à l'exclusion de l'ovipositeur), n'empêche ni le développement, ni l'efficacité du bourrelet glandulaire qui est protrusé sans arrêt; quelques-unes de ces ♀ opérées ont eu, après un accouplement plus ou moins fictif, un comportement de ponte "à vide": La présence d'ovules à pondre ne commande pas les phénomènes d'attraction.

Rôle du système nerveux: L'ablation des cérébroïdes, ou leur déconnection, supprime tous les éléments du comportement reproducteur. Le bourrelet ne sort pas mais il est efficace si on le fait saillir par pression.

L'ablation du ganglion abdominal terminal empêche, à la fois, protrusion et ponte. La section des connectifs, en avant de ce ganglion, supprime la protrusion mais permet l'accouplement et même la ponte.

Un résultat analogue, moins constant, moins sûr, mais sans lésion nerveuse, a été obtenu par accouplement prématuré avant la mue nymphale, et prolongé jusqu'à la sénéscence de la ♀ qui pond alors rapidement sans protruser.

L'étude de l'avenir des pontes déposées dans ces conditions, semble indiquer une fécondabilité et une viabilité diminuées.

Le déclenchement initial des phénomènes attractifs se produirait, d'après nos observations à partir de stimulations cérébrales lancées dès la première heure de la vie imaginale.

SUR QUELQUES MECANISMES DES CONTACTS TROPHALLACTIQUES CHEZ LES GUEPES SOCIALES DU GENRE *VESPA*

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Nous avons effectué une étude systématique des mécanismes et des polarités qui es vroduisent au cours des contacts trophallactiques chez les Vespinae, au moyen de techniques a riées:

—L'analyse sur films pris en vitesse accélérée,

—Des sections d'antennes et de palpes,

—L'utilisation d'isotopes radioactifs (^{198}Au, ^{32}P, ^{35}S).

Nous avons ainsi montré que le contact trophallactique peut résulter de motivations extrèmement différentes:

(*a*)—l'obtention de régurgitations de nourriture à partir du jabot entre ouvrières;

(*b*)—La recherche de contacts sensoriels très bien adaptés et hiérarchisés, et par suite l'établissement de dominances.

La recherche des régurgitations est une motivation puissante qui provoque des postures d'offre et de sollicitation absolument caractéristiques. La solliciteuse qui n'a pas une hiérarchie suffisante dans la société ou qui manque de nourriture finit toujours par adopter une posture de sollicitation couchée, alors que ses antennes et ses palpes stimulent une donneuse apparemment passive.

En résumé, l'antenne externe de la solliciteuse vient stimuler avec précision la langue de la donneuse dans l'espace intermandibulaire. Elle est responsable de l'obtention continue des régurgitations de nourriture. L'antenne interne permet le maintien du contact social proprement dit par une stimulation appropriée des palpes de la donneuse. Les palpes sont toujours érectés et orientés vers le point de jonction des mandibules: ils ont probablement un rôle gustatif.

La donneuse est apparemment passive sous l'effet des stimulations pressantes de la solliciteuse. Elle indique à cette dernière la fin de la régurgitation en ramenant ses antennes dans le plan de jonction des mandibules.

Ce schéma se modifie selon les rapports de dominances qui existent entre les 2 partenaires. Ainsi, un individu dominant manifeste son rang hiérarchique par des manifestations diverses:

—Lorsqu'il demande sa nourriture à une ouvrière de rang inférieur, il l'aborde de front en stimulant activement les palpes de chaque côté; ou alors, il maintient une patte et son antenne externe sur les pièces bucalles ou même le front de l'individu inférieur.

—Dans un relai trophallactique, il prend d'autorité la place d'une solliciteuse moins dominante auprès de la donneuse. Au cours de l'acte trophallactique, il éloigne une intruse éventuelle par des contacts antennaires ou mandibulaires vigoureux.

—Il monte sur le dos des individus inférieurs et leur mordille les ailes ou toute autre partie du corps.

Les stimulations complexes de l'acte trophallactique ne sont pas innées, mais doivent s'acquérir à partir de l'éclosion imaginale ou de la chute de l'opercule, par apprentissage. La jeune guêpe est en effet alimentée de force dans son cocon, ou juste à sa sortie, par de véritables nourrices, sans qu'elle l'ait sollicité. Ces dernières l'imprègnent en même temps de l'odeur spécifique du guêpier. Ce n'est que I à 2 jours après son éclosion que la jeune guêpe est capable de solliciter activement des contacts nutritifs et sensoriels.

Dans certaines conditions défavorables, la fondatrice doit solliciter les régurgitations des ouvrières selon le même processus que ces dernières. Mais, elle se fait nourrir passivement lorsqu'elle est dominante dans le nid en place.

Les mâles sont parfaitement négligés par les ouvrières et s'approvisionnent essentiellement en s'intercalant dans des contacts trophallactiques entre ouvrières et en faisant régurgiter les larves de façon permanente.

COMMUNICATION IN THE TERMITE *ZOOTERMOPSIS ANGUSTICOLLIS* (HAGEN)

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Koenig in 1779 observed a species of *Hodotermes* in which the soldier termites hit their mandibles against dry leaves when they were disturbed, producing a clearly audible sound. There are many similar records in the literature from many termite species, and the sound has mostly been assumed to be an alarm signal. There are also jerking movements common in termites during which no sound has been detected. Emerson (1929) suggested that an odour stimulus might be released during such movements.

The jerking or oscillatory movements of the damp-wood termite *Z. angusticollis* have been investigated by the author (1) (2) (4), using cine-photography and sound-recording techniques. Recordings of the intervals between sounds were made from a tape-recording, using a transducer to mark a revolving smoked drum.

It was found that the soldiers produced sound by hitting their mandibles or head capsule against the floor and roof of galleries, while the other castes hit their heads against only the roof of the galleries. The associated jerking movement, which cine photographs show is made almost entirely by extension and contraction of the forelegs, was named the Vertical Oscillatory Movement (V.O.M.).

The V.O.M. is made when termites are disturbed. It was found that they are sensitive to substratum vibration but not to airborne sound. Experiments showed that under the influence of substratum vibration produced by tapping, negative phototaxis, positive geotaxis, positive chemotaxis (to pheromonal substances), and positive thigmotaxis are more marked in the termites. This suggests that vibration can start or intensify patterns of behaviour that will take the termites downwards into cracks and into the less accessible parts of the nest.

An electrophysiological investigation (3) has shown that the subgenual organ is well adapted to register the particular pattern of the sounds, which consists of a brief but very rapid series of taps followed by an interval of about $\frac{1}{2}$ a second (see table). There seems to be no information contained in variations in the sound pattern, these being mainly temperature-dependent.

	For subgenual organ at 21°C	*Of sound*
Optimal frequency	~1,150 cycles/sec.	900-1,750 cycles/sec. mean ~1,140 cycles/sec.
Fastest pulse rate	30/sec.	24/sec at 21°C 36/sec at 23°C
No. of pulses	1-10 before adaptation begins (at 30 pulses/sec.)	1-8 mostly 2 or 3
Interval between groups of pulses	⩾0·5 sec. before adaptation ceases	0·5 sec. at 21°C

Table showing some of the ways in which the subgenual organ is tuned to the sound pattern in *Z. angusticollis*

In the Complex Oscillatory Movement (C.O.M.) the body is shaken vigorously to and fro and up and down, but no sounds are produced. Evidence was found that this movement occurs after the laying of an odour trail, for which some confirmation is found in the recent work of Stuart (1963) and Lüscher and Müller (1960). When a group of termites disturbed by the C.O.M. of others were given the opportunity to follow an odour trail they did so, but when given the choice of either following the trail or going downwards they took the latter course (unpublished). This suggests that the C.O.M. is solely a means of arousing other termites.

The Longitudinal Oscillatory Movement is a rapid to and fro oscillation of the body which occurs only when a termite touches a moving object or a surface with certain chemical characteristics (e.g. possibly an insect of some other species). It appears to be a simple reflex response to a relatively low-level stimulus to antennal sensilla.

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FORMS AND PATTERNS OF INSECT LOCOMOTORY MOVEMENTS

LAUFKOORDINATION UND REGELUNG DER BEINSTELLUNG BEI DER STABHEUSCHRECKE *CARAUSIUS MOROSUS*

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Nach v. Buddenbrock (1) bewegen sich bei einer laufenden Stabheuschrecke Vorder- und Hinterbein einer Körperseite in gleicher Phase mit dem Mittelbein der anderen Seite und in Gegenphase zu den drei übrigen Beinen, die unter sich wieder in gleicher Phase laufen. Nach Amputation beider Mittelbeine ändert sich die Koordination. Jetzt laufen Vorder und Hinterbein einer Seite fast in Gegenphase. V. Buddenbrock erklärte dieses Ergebnis mit der durchaus plausiblen Annahme, daß bestimmte Sinnesorgane in den Beinen durch deren rhythmische Bewegung gereizt werden und die gegenseitige Phasenlage der Beine determinieren. Ihr fehlender Einfluß muß sich in einer geänderten Koordination bemerkbar machen.

Es gibt noch zwei weitere Erklärungsmöglichkeiten für dieses Versuchsergebnis.

1. Mehrere Autoren (2) haben darauf hingewiesen, daß die nach Amputation der Mittelbeine auftretende neue Koordination dem Tier überhaupt erst das mechanische Gleichgewicht wiedergibt; denn wenn die Beine in der alten Weise weiterliefen, müßte das Tier bei jedem Schritt zur Seite kippen. Es wäre nun denkbar, daß diese veränderten mechanischen Bedingungen von Receptoren in den restlichen Beinen gemessen werden, die nun dauernd eine das Gleichgewicht erhaltende Koordination erzwingen. Die Ursache wäre also die nach Mittelbeinverlust geänderte *mechanische Situation* und weniger der Ausfall der Afferenzen aus den Mittelbeinen. In meinen Versuchen waren die Stabheuschrecken durch einen Halter relativ zur Unterlage fixiert (5). Auch unter diesen Bedingungen ändert sich die Koordination nach Mittelbeinverlust. Da die Beinamputationen das Gleichgewicht der fixierten Tiere nicht beeinflussen können, ist die Koordinationsumstellung *keine Reaktion auf die augenblickliche Gleichgewichtslage.*

2. Hughes hat 1952 ebenfalls darauf hingewiesen, daß die Beinkoordination stark geschwindigkeitsabhängig ist. Wie man außerdem weiß läuft ein Insekt, dessen Mittelbeine amputiert sind, im Durchschnitt langsamer als ein intaktes Tier. Vielleicht erweist sich die geänderte Koordination nur als eine Folge geringerer Laufgeschwindigkeit?—Zur Prüfung dieser Möglichkeit registrierte ich die Beinkoordination intakter und mittelbeinloser Stabheuschrecken bei möglichst vielen Laufgeschwindigkeiten (fig. 1). Zur Kennzeichnung der Koordination zweier Beine sei hier ihre Phasenverschiebung angegeben. Sie ist die Zeitdifferenz zwischen den Abhebzeitpunkten zweier Beine. Der Vergleich der Phasenverschiebungen bei einer Stabheuschrecke vor und nach Mittelbeinautotomie *bei der gleichen Laufgeschwindigkeit* (fig. 1) zeigt, daß die Vorderbeine nach der Autotomie etwa die gleiche Phasenverschiebung zum Hinterbein einnehmen, die vorher die intakten Mittelbeine innehatten. Die Mittelbeinstummel bewegen sich ebenfalls in derselben Phase wie zuvor die intakten

Mittelbeine, so daß Vorderbeine und Mittelbeinstummel nun fast in Phase schwingen. Das ist bei allen untersuchten Geschwindigkeiten der Fall.

Die hier beschriebene Änderung der Koordination ist also weder als Folge geringerer Laufgeschwindigkeit noch als Reaktion auf das gestörte mechanische Gleichgewicht zu erklären, sondern stellt sich automatisch nach Ausfall der Afferenzen aus den amputierten Beinen ein.

Diese Afferenzen müssen eine mit der rhythmischen Bewegung der Beine zusammenhängende Größe repräsentieren. Dies zeigt folgender Versuch, den schon v.Buddenbrock, allerdings am frei laufenden Tier, ausgeführt hat. Bietet man den Mittelbeinen eine kleine Plattform aus weichem Holz, so krallen sie sich darin fest und scheren aus der Koordination aus. Die vier restlichen Beine laufen weiter als seien die Mittelbeine amputiert (fig. 2).

Pringle hat 1938 drei Borstenfelder an den proximalen Beingelenken der Schabe entdeckt und elektrophysiologisch untersucht. Bei der Stabheuschrecke befinden sich ebenfalls drei Borstenfelder an den entsprechenden Stellen. Die Borsten des Feldes 1 am Trochanter (fig. 2, Einschubbild) werden abgebogen und gereizt, wenn das Bein nach oben schwingt. Die beiden coxalen Felder (2 und 3) messen die Stellung des Subcoxalgelenks. Sie werden gereizt, wenn das Bein nach vorn schwingt. Diese Sinnesorgane erscheinen hervorragend geeignet, die Phase eines Beins während des Laufs zu messen und die Koordination entsprechend zu beeinflussen. Rasiert man alle Borstenfelder der beiden Mittelbeine ab, so tritt jedoch nicht die gleiche Koordination wie nach Mittelbeinamputation auf (fig. 2).

Die von mir untersuchten Borstenfelder determinieren die Phasenbeziehung der Beine also nicht. Sie zeigen aber andere interessante Leistungen:

Die Borstenfelder 1 und 2 (für Feld 3 konnte keine Leistung nachgewiesen werden) aller Beine sind Glieder von Regelkreisen: sobald sie gereizt werden, wirken sie im Sinne einer Verminderung des Reizes auf die Muskulatur desjenigen Gelenks, dessen Stellung sie messen. Feld 1 stabilisiert also die Stellung des Coxa-Trochantergelenks, und Feld 2 stabilisiert die

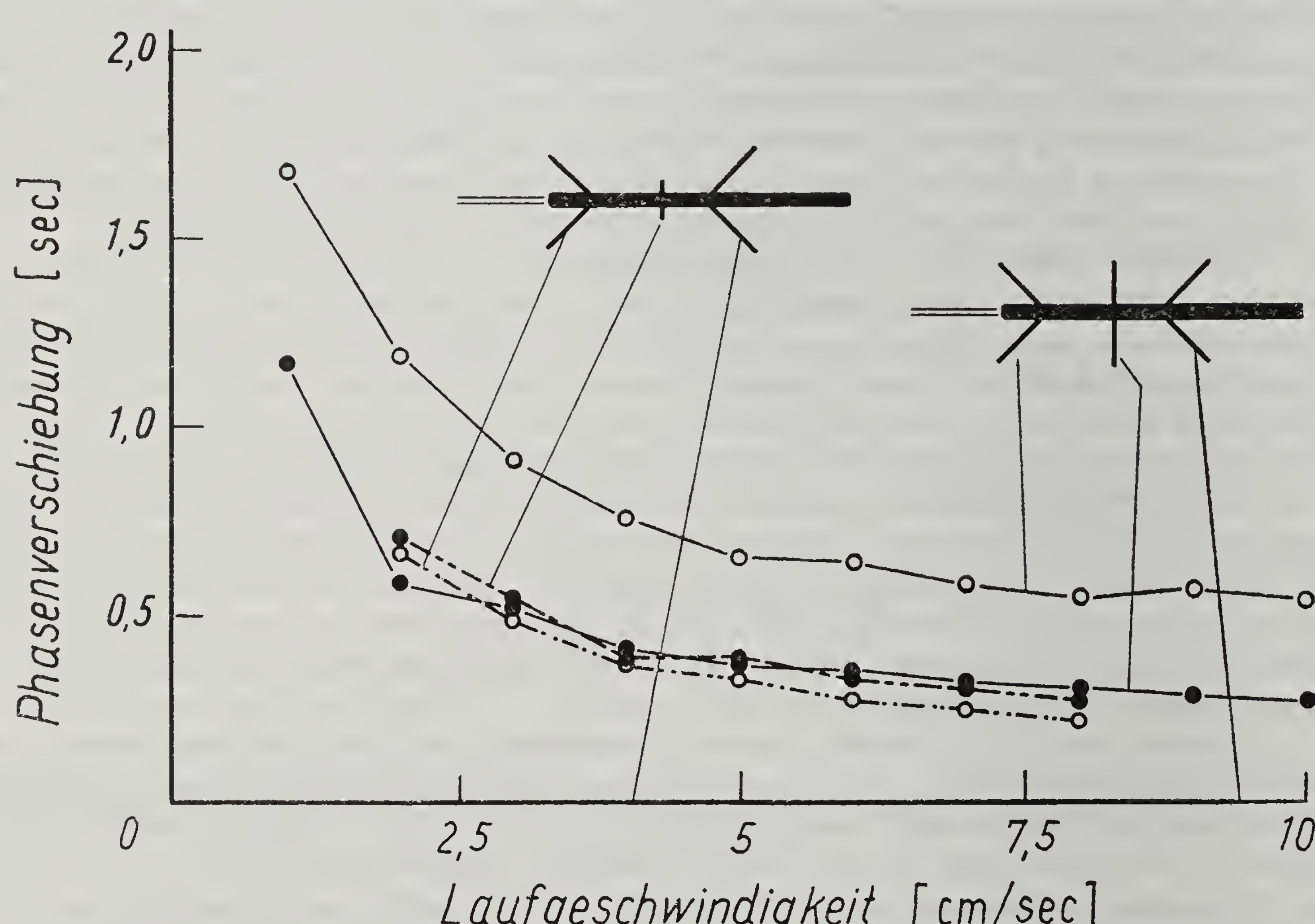

Fig. 1. Die Phasenverschiebung vom linken Vorder- (o) und Mittelbein (•) gegenüber dem linken Hinterbein als Funktion der Laufgeschwindigkeit. Bezogen wird stets auf den Abhebzeitpunkt des Hinterbeins (in Abszissenhöhe). ——— intaktes Tier. —..—..—Vorderbein und mit Balsaholzzeigern verlängerter Mittelbeinstummel nach Autotomie beider Mittelbeine. Die Punkte stammen von einem Tier; sie stellen Mittelwerte aus nach Geschwindigkeitsklassen zusammengefaßten Meßwerten dar.

Stellung des Subcoxalgelenks gegen stellungsändernde Einflüsse. Solche Einflüsse können sowohl die rhythmischen Bewegungsimpulse beim Laufen (1) als auch von außen angreifende Kräfte (2) sein. In beiden Fällen muß die Stellungsänderung sich vergrößern, wenn die Borstenfelder zerstört sind.

1. Beim laufenden Tier bewirkt eine Zerstörung z.B. des Borstenfelds 2 des linken Mittelbeins eine vergrößerte Schwingungsamplitude. Außerdem erscheint die ganze Schwingung weiter nach vorn verlagert. Daher berührt das operierte Bein jetzt häufig das nächstvordere und krallt sich manchmal daran fest, so daß das Tier stolpert. Entsprechend schwingt das Bein weiter nach oben aus, wenn das Borstenfeld 1 am Trochanter abrasiert ist.—Die beiden Borstenfelder dämpfen also die Amplitude der Beinschwingung nach vorn bzw. oben.

2. Eine äußere Kraft ist vor allem das Gewicht des Rumpfs. Bei einer stehenden Stabheuschrecke muß jede Bewegung des Rumpfs relativ zu den Tarsen die Stellung der Beingelenke verändern. Da die Borstenfelder die Gelenkstellung regeln, stabilisieren sie gleichzeitig die Lage des Körpers zu den Tarsen. Dies gilt für jede beliebige Stellung des Tiers zur Schwerkraft oder einer anderen mechanischen Kraft. Der zwischen den Beinen aufgehängte Rumpf der Stabheuschrecken sinkt nach Zerstörung aller Borstenfelder 1 und 2 unter seinem eigenen Gewicht 2,4mal so weit nach unten wie normal. Das bedeutet, daß die Borstenfeldregelkreise 59% der Auslenkung kompensieren.

Nach weiteren Versuchen sind die Regelkreise der verschiedenen Beine nicht miteinander gekoppelt. Der Weg der Regelkreise führt vom Borstenfeld zum dazugehörigen Thorakalganglion und von dort aus direkt zur Muskulatur. Möglicherweise geht ein weiterer Zweig über die Cerebralganglien.

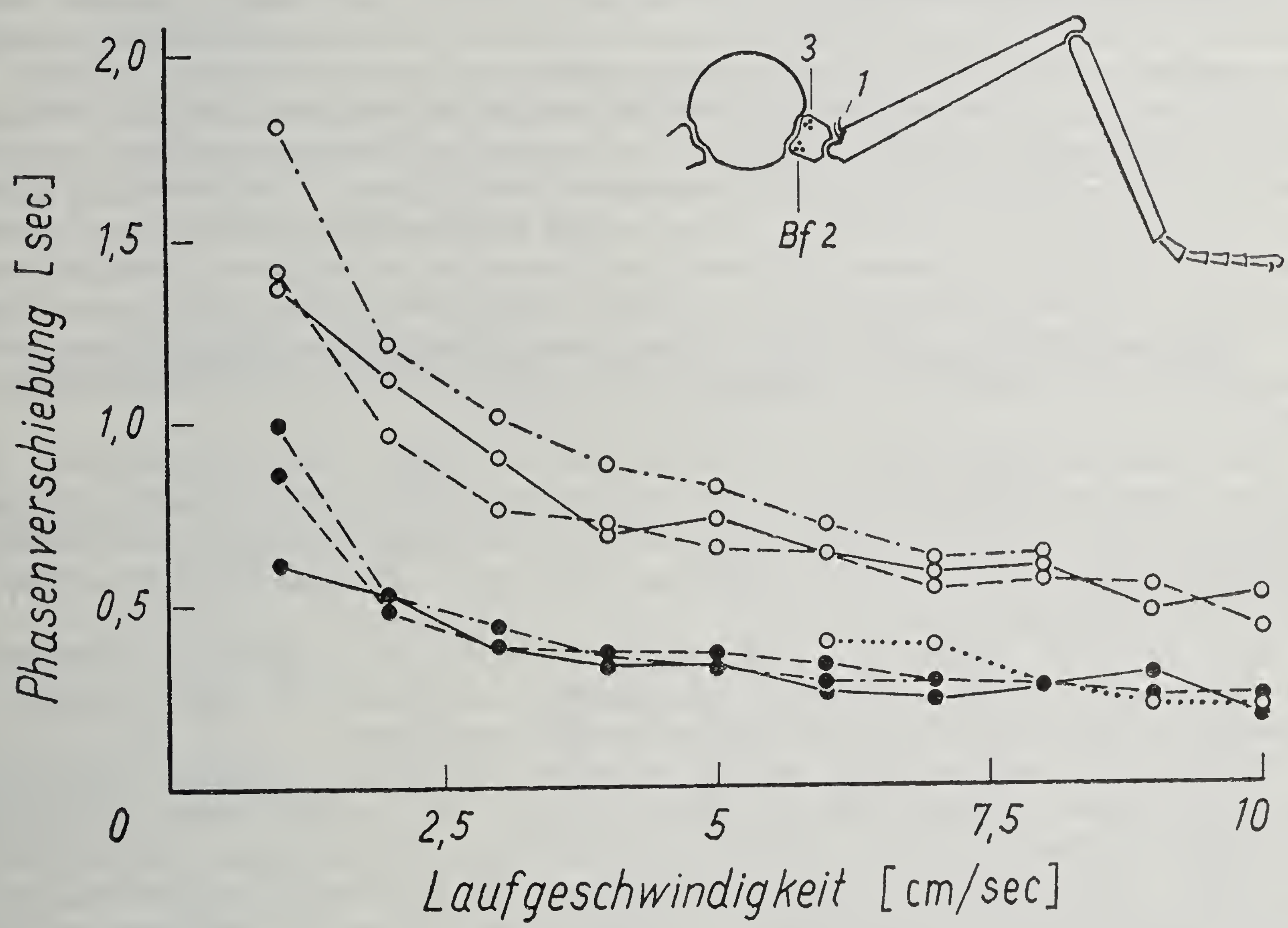

FIG. 2. Wie fig. 1 ——— intaktes Tier. — — — — Borstenfeld (Bf) 2 beider Mittelbeine abrasiert.—.—.—Bf 1, 2 und 3 beider Mittelbeine abrasiert. . . . . linkes Vorderbein, wenn sich beide (intakten) Mittelbeine an einer Plattform festkrallen. Einschubbild: ein linkes Bein mit den drei Borstenfeldern.

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MAGNETFELD-ORIENTIERUNG VON INSEKTEN

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Nach Versuchen von F. Schneider (1961-1964) werden Maikäfer (*Melolontha vulgaris* F.) bei der Ruhestellung und beim Abflug von künstlichen Magnet- und elektrischen Feldern beeinflußt. Entflügelte Imagines von Macrotermitiden und anderen Termiten bevorzugen in ihrem Nest N/S- oder O/W-Richtung (G. Becker 1963). Im künstlichen, stärkeren Feld eines Eisenmagneten folgen sie diesem; in einem MU-Metall-Kasten, der das Magnetfeld der Erde abschirmt, nehmen sie dagegen beliebige Ruhe-Richtungen ein.

Dipteren zeigten beim Landen und in Ruhe, Cerambyciden-Imagines und Schaben in Ruhestellung, Heimchen und Heuschrecken beim Springen und Landen eine Bevorzugung der N/S- und O/W-Richtung, und zwar zu verschiedenen Tageszeiten und bei Sonnenlicht wie in künstlichem Licht (G. Becker 1963, 1964). Dipteren reagieren auf das Feld von Eisenmagneten und in stromdurchflossenen Spulen.

Das Verhalten von Dipteren ist inzwischen auch im Laboratorium genauer untersucht worden. Imagines von *Calliphora erythrocephala* und *Musca domestica* L. wurden in fensterlosen Räumen in Holzkästen nach Aufscheuchen in ihrer Landerichtung auf waagerechter Unterlage fotografiert. Dabei wurde der Kasten bei der Mehrzahl der Versuche von unten durch eine Milchglasscheibe erleuchtet. Die Kastenwände hatten meist einen Winkel von 30° zur N/S-Richtung. Die Richtung der nicht während der Aufnahme bewegten Fliegen konnte auf $\pm 1°$ genau ausgemessen werden.

Obwohl die Tiere offensichtlich durch Kastenwände, andere Fliegen, chemische Reize und anderes in ihrer Richtung beeinflußt waren, hat sich eine statistisch einwandfrei gesicherte Bevorzugung der N/S- und der O/W-Richtung ergeben.

Das Reagieren auf das Magnetfeld der Erde wurde ferner dadurch zweifelsfrei bewiesen, daß das Versuchsgefäß mit den Fliegen in das Zentrum von Helmholtz-Ringen gebracht wurde, mit deren Hilfe das Magnetfeld kompensiert werden kann. Die Aufhebung gelang darin bis auf ein Restfeld von rd. 5%. Abwechselnde Aufnahme-Serien mit und ohne natürliches Erdfeld ergaben im ersteren Fall deutliches Bevorzugen der N/S- und O/W-Richtung, im letzteren eine andersartig geordnete Richtung. Subtraktion beider Wertegruppen zeigte für *Calliphora* und für *Musca* sehr ähnliche Häufigkeitsgipfel in N/S- und O/W-Richtung sowie Nebengipfel der Häufigkeitsverteilungskurve in Winkeln von 45° zu den Hauptrichtungen (Bild).

Die Häufigkeitsgipfel liegen nur teilweise genau in N/S- und O/W-Richtung. Bei manchen Versuchsreihen ist ein Gipfel oder sind beide geteilt, indem der Abstand der Doppelgipfel von N/S oder O/W 10 bis 15° beträgt. Bisweilen ist nur einer der Teilgipfel ausgeprägt. Ähnliches Verhalten wurde auch bei *Sarcophaga* beobachtet. Die Ursache für diese Erscheinung muß noch geklärt werden.

An senkrechten Wänden in N/S-Richtung macht sich im Vergleich zu Wänden in O/W-Richtung die Hauptrichtung des Magnetfeldes auf Fliegen nur wenig bemerkbar. Offensichtlich überwiegt dabei der Schwerkrafteinfluß weitgehend.

Die Fähigkeit zum Reagieren auf das natürliche und auf ein künstliches Magnetfeld scheint eine allgemeine Eigenschaft der Insekten zu sein. Die Reaktion tritt in Konkurrenz mit anderen Einflüssen nur unter bestimmten Verhältnissen in Erscheinung. Die Magnetotaxis ist bei Untersuchungen über das Verhalten und die Physiologie der Insekten künftig zu beachten und genauer zu untersuchen. Auslösung und Vorgang des Reagierens bedürfen noch der Erklärung.

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FLIGHT BEHAVIOUR IN SOME ANOBIID BEETLES

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The death watch beetle, *Xestobium rufovillosum*, usually regarded as incapable of flight, was shown to be capable of flight under certain conditions. Free, rising flight occurred only when beetles fell from a surface warmed to 30-40°C in an ambient temperature above 22°C (upper limit was not determined). On a rotating mill flights up to 10 minutes were recorded. Tethered flight was shown to have the same characteristics as flight on a mill. Wing-beat frequencies of 3 anobiid beetles were: *Xestobium*—70/85c/s; *Anobium punctatum*—90/130c/s; and *Ernobius mollis* a strongly flying anobiid, —70/90c/s. Characteristics of wing shape, stroke angle, stroke plane angle and wing twisting movements were similar in the 3 species. Tethered flight started at 17-18°C; the frequency rose with temperature to 22°C and was then relatively constant to 30°C (fig. 1). It is argued that 22° might be the threshold for free flight. Temperatures in infested buildings are generally below this, which might account for the observed behaviour of *Xestobium* in falling to the floor early in the emergence period with the female still containing unlaid eggs (Harris, 1964).

Flight willingness, tested by tethered flight, was high in newly emerged males. Results of testing beetles collected from the floor of Westminster Hall, London, are shown in Table I. There was an indication that in females flight-willingness was highest in beetles which had laid some eggs.

Histological examination of fibrillar flight muscle of the 3 anobiids showed that all were similar in sarcosome size and content. No difference was detected between muscles of flying and non-flying *Xestobium.*

Flight in *Xestobium* is possible and could explain aspects of the distribution of the insect out of doors, but the extent to which it occurs in nature is still unknown.

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Table I

Flight-willingness of individual *X. rufovillosum* from Westminster Hall, tested 1 day after collection

Date tested	*Males*			*Females*			
	+Spont.	*+Stim.*	*Neg.*	*+Spont.*	*+Stim.*	*Neg.*	*% females flight-willing*
15-19 April	3	0	1	—	—	—	—
25-29 April	4	0	6	6	2	11	42%
30 April-4 May	1	0	11	11	1	11	52%
5- 9 May	0	0	20	47	5	50	51%
10-14 May	—	—	—	34	10	72	38%
21-26 May	—	—	—	0	5	31	14%
Totals	8	0	38	98	23	175	41%

+Spont. ... Spontaneous tethered flight
+Stim. ... Tethered flight after stimulation
Neg. ... Flight not elicited
— ... No beetles tested

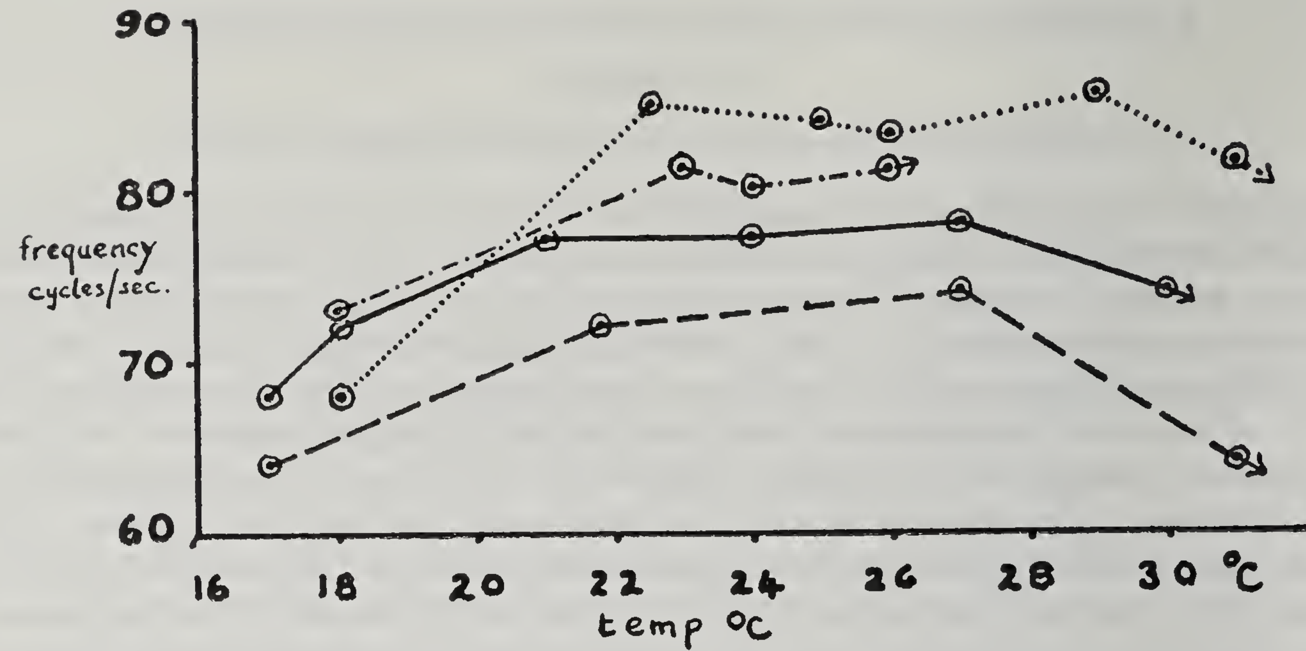

FIG. 1. *X. rufovillosum:* Change of wing beat frequency with temperature in four individuals.

THE INFLUENCE OF INCREASING ELEVATION (TO 14,000 FEET) ON BEHAVIOUR, FORAGING AND DISEASE OCCURRENCE IN THE HONEY BEE, *APIS MELLIFERA*

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According to Mani (4), timber-line on mountains is the threshold of an almost unexplored world of insects. In this biotic province between timberline and the tops of the mountains, altitude is a profound modifier which affects all other factors of this specialized alpine or nival environment.

In order to study the effects of high elevation and the alpine life zone on the honey bee, *Apis mellifera*, colonies were transported from a control apiary in favourable surroundings at 5,200 feet (1585 meters) to various levels between 9,500 feet (2896 meters) and 14,000 feet (4267 meters). Studies were made in June through August for four consecutive years (1961-1964). Honey bees have not been maintained at elevations above 9,500 feet (2, 4, 6).

Even though there is less oxygen available to both the adults and immature bees, along with greatly reduced temperatures, brood development was not significantly retarded in comparison with colonies at the control apiary. Egg laying by the queens continued at a near normal rate with production increasing during the first portion of the season at all elevations.

Utilizing adult mortality traps devised by Gary (3), it was observed that contrary to an earlier hypothesis, adult worker mortality was approximately the same regardless of elevation. No immature bee mortality was noted except in populations which were inoculated with pathogenic bacteria. A serious loss of productive queens was sustained during the following winter in colonies that were moved from high altitude sites to the control apiary at 5,200 feet.

In the gathering of pollen, the worker bees are capable of bringing in large pollen loads even at 14,000 feet. An adequate supply of brood rearing pollen was available at all elevations from plants indigenous to each area. Qualitative and quantitative measurements of bee collected pollen were made with pollen traps developed by Townsend (5). Nectar is also available at all sites and bees have been seen probing the blossoms. Many workers had full honey stomachs. Over 50 species of nectar and/or pollen plants have been studied in the

alpine and sub-alpine regions. Foraging bees have been observed at distances of one mile (1609 meters) from the hive at the highest elevations, while at the 10,000 foot (3048 meters) level they travel over 2·5 miles (4023 meters) from the parent colony.

The customary driving of the drones from the colony after the advent of freezing temperatures did not occur even though the minimum nocturnal temperatures at 14,000 feet were often 32 degrees F. (0 degrees C.). General observations indicate that the males are driven out only after a combination of low temperature and reduced day length.

At lower altitudes, honey bees quickly return from foraging activities in the field as a result of changes in climatic conditions. In the alpine, they apparently adjust to the more severe environment and have been observed foraging for nectar and/or pollen during light rain, low light intensity, and at temperatures as low as 45 degrees F. (7·2 degrees C.). Swarming normally occurs during the spring and summer when the hive population is under rapid expansion. Above 10,000 feet the swarming impulse is present in colonies even when the night temperatures are below freezing. Colonies have swarmed and the virgin queens successfully mated in a few cases.

Bailey (1) and others have recorded the fact that the external environment greatly influences the occurrence and progress of European foulbrood disease, *Streptococcus pluton*. Twelve EFB inoculated colonies were located at 5,200, 9,800, 12,800, and 14,000 feet on Mount Evans, Colorado. All inoculated colonies developed EFB symptoms. Even though the larvae at the higher elevations were under increased stress, increasing elevation did not significantly increase the occurrence of the disease.

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CONTRIBUTION A L'ETUDE DES REGULATIONS DU COMPORTEMENT ALIMENTAIRE DES LARVES D'ODONATES

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Les travaux de divers électrophysiologistes ont montré qu'il existe une liaison temporelle entre les phénomènes électriques décelables dans le lobe optique et certains phénomènes électriques décelables dans la chaîne nerveuse abdominale des Insectes.

Les morphologistes ne sont pas tous d'accord sur la dénomination des muscles du labium des Odonates et la mécanique de leur fonctionnement pose encore de nombreux problèmes. Depuis Amans (1) repris récemment par Snodgrass (4) plusieurs auteurs ont fait intervenir un mécanisme hydraulique dans la projection du masque; ils ont en général situé son origine dans le diaphragme qui, chez les seuls Anisoptères, barre la partie antérieure du IVè ou du Vè segment abdominal.

Une analyse cinématographique nous a montré chez *Aeshna cyanea* que le premier temps de capture est une ouverture des crochets labiaux. Ensuite le postmentum est projeté vers l'avant et le prémentum se déploie plus tardivement. Un mécanisme hydraulique assure la poussée maximum du masque au moment de l'augmentation de pression hémolymphatique dans la capsule céphalique et permet le retrait du masque par élasticité de la membrane articulaire au moment où la pression cesse. Ce mécanisme n'est pas le seul fait du diaphragme sus-désigné, mais le résultat d'une coordination de nombreuses contractions musculaires abdominales facilitées par l'existence de muscles transverses (VIè segment abdominal) et de diaphragmes thoraciques reconnus en 1917 par Brocher (2).

Nos recherches prouvent que tous ces muscles transverses et diaphragmes sont innervés

par des dépendances du nerf médian. Mais si le dispositif hydraulique en rapport avec le nerf médian joue certainement un rôle de facilitation de la projection ou du retrait du masque, il ne représente qu'une partie du mécanisme coordonné de fonctionnement du dispositif de capture.

En effet nous attribuons aux muscles de la base labiale des rôles importants et quelque peu différents de ceux attribués par nos prédécesseurs. Nous pensons également que l'apodème hypopharyngien caractéristique des larves d'Odonates décrit depuis longtemps et sur lequel Munscheid (3) a bien insisté, joue un rôle important dans le fonctionnement du labium.

Pour nous, le muscle dit "fléchisseur du prémentum" se contracte dès le début de la projection et tire vers le bas l'apodème hypopharyngien qui pivote autour de sa base antérieure rendue fixe par la contraction du muscle rétracteur de l'hypopharynx (ce muscle d'ailleurs ne s'attache pas sur le tentorium contrairement à l'opinion de Snodgrass mais sur la base d'articulation maxillo-labiale que sa contraction rend également fixe). Ce mouvement permet la bascule vers l'avant du postmentum. Lors de la fermeture du masque, l'apodème remonte par élasticité de la membrane articulaire favorisée par la diminution de la pression sanguine et le muscle fléchisseur du prémentum joue son second rôle de fermeture du masque. Il est aidé dans son fonctionnement par les muscles situés dans l'articulation entre post et prémentum. Le muscle extenseur du prémentum a un rôle bien plus simple car une de ses attaches est fixe: l'attache proximale sur le tentorium.

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Fig. I. Représentation schématique d'une dissection de la région latéroventrale antérieure du Vè segment abdominal d'une larve d'*Aeshna cyanea.*
An: anastomose entre nerf antérieur du Vè segment et nerf médian; C: cuticle; D: diaphragme abdominal et son innervation; Na: nerf antérieur du Vè segment abdominal; Nm nerf médian entre IVè et Vè segments; Nt: nerfs du tergite; T: trachées.

Fig. II. Larve d'*Aeshna cyanea*—Représentation schématique d'une dissection de la région articulaire du postmentum sur le crâne.
Ah: apodème hypopharyngien; An: "ancre" de l'apodème hypopharyngien; C: connectif collaire; Cp: connectif périoesophagien; Gso: ganglion sous oesophagien; Hy: nerf hypopharyngien; L1: nerf labial externe qui innerve le muscle rétracteur de l'hypopharynx; L2: nerf labial interne; Md: nerf mandibulaire; Mep: muscle extenseur du prémentum; Mfp: muscle fléchisseur du prémentum; Mrh: muscle rétracteur de l'hypopharynx; Mx: nerf maxillaire; Pm: postmentum; Te: tentorium; Tg: trachée du ganglion sous oesophagien.

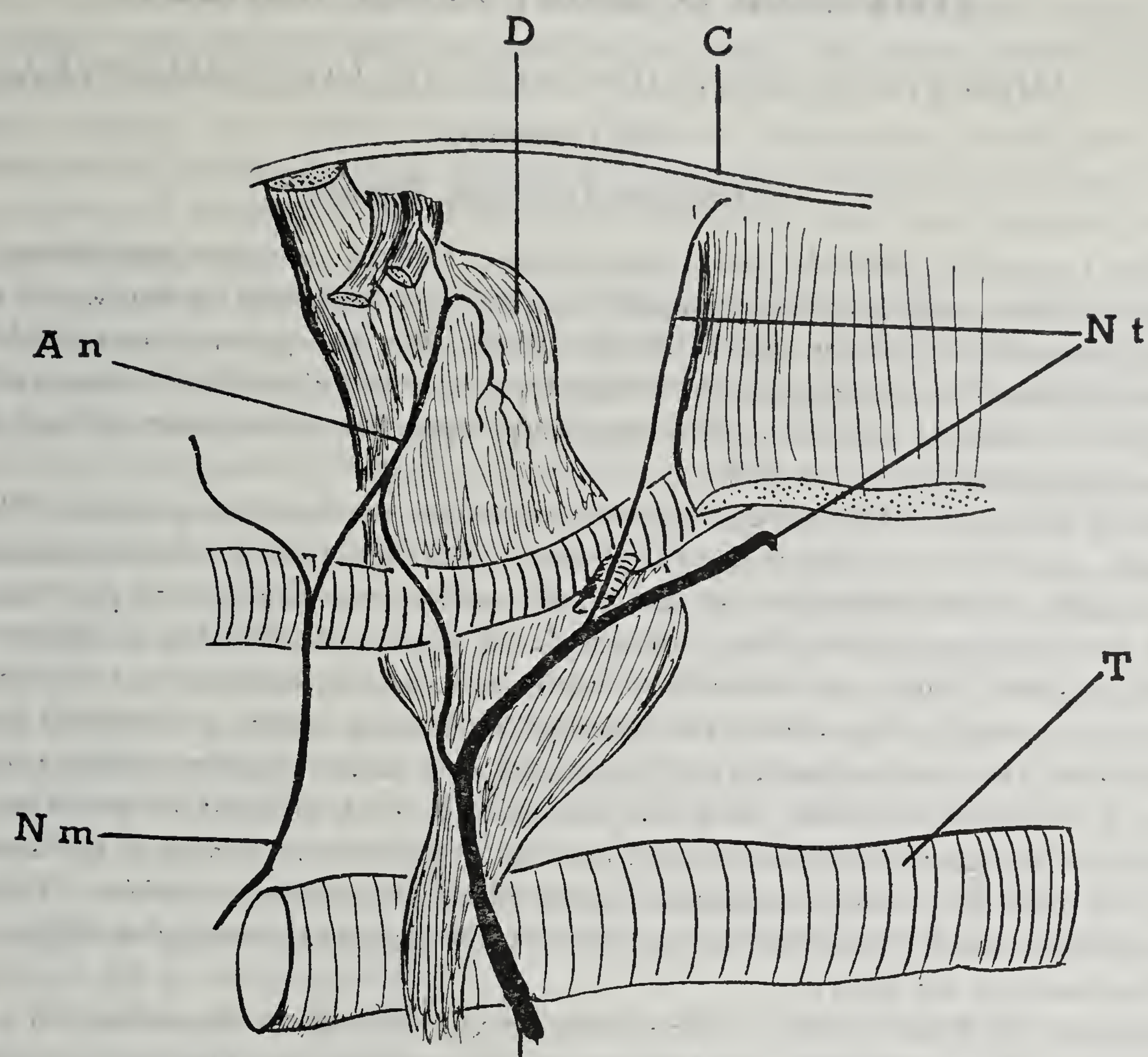

Figure 1

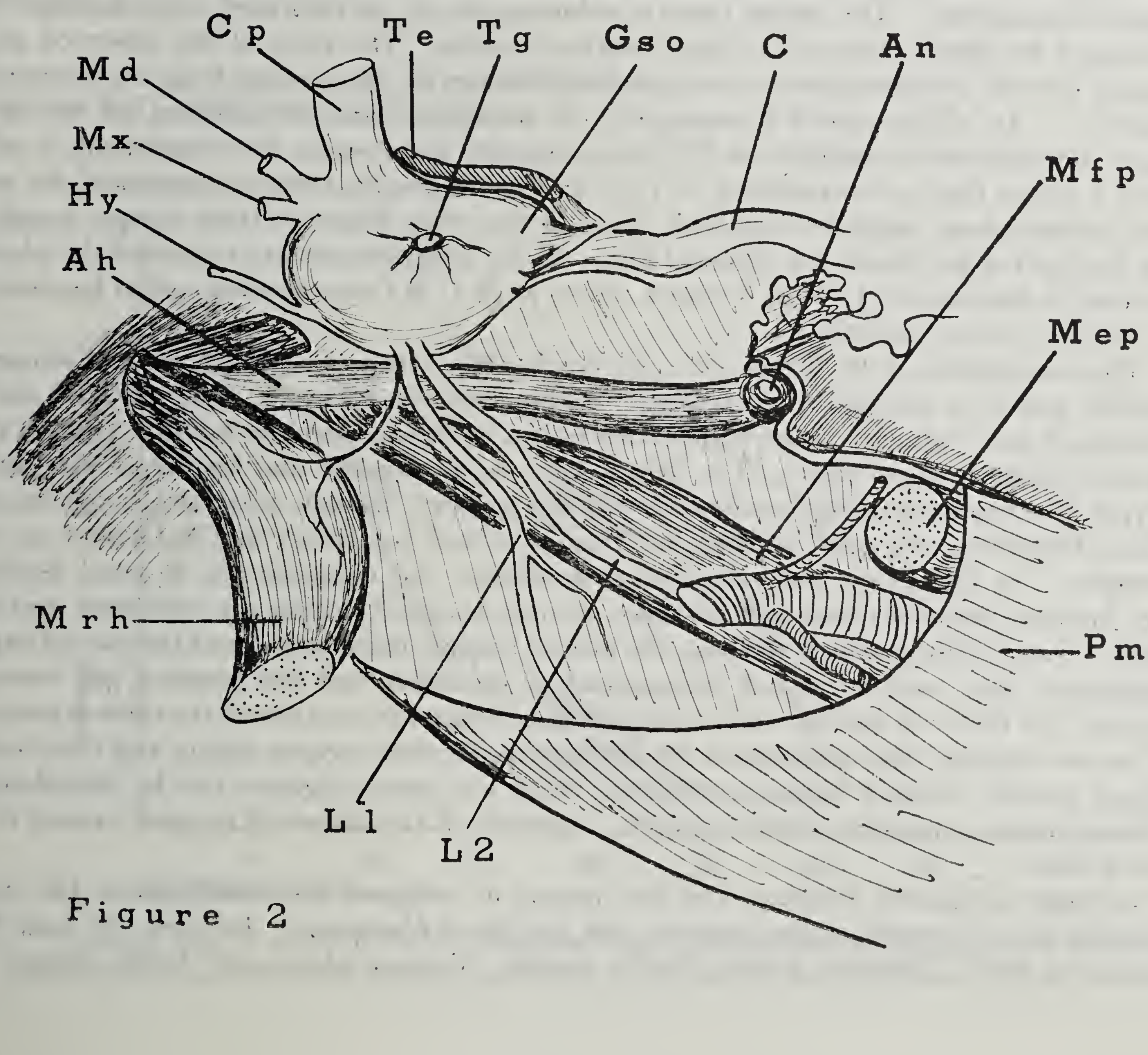

Figure 2

BEHAVIOUR IN SHORT RANGE DISPERSAL

MIGRATION MOVEMENTS OF AQUATIC HEMIPTERA

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Unlike terrestrial animals, pond populations live in constant conditions of humidity, pH, and to a lesser extent of temperature, and are not subjected to the water movements of rivers and streams nor to the effects of the tides. For the greater part of the year, insect populations of ponds are unmodified by migration and are ideal for the study of the effects of the annual and diurnal variations of temperature upon the movements of individual animals as well as the population as a whole.

Levels of Activity. Water bugs and water beetles are inactive at about 0°C but become increasingly more active as the temperature rises. Except at very low temperatures, *Notonecta glauca* normally floats motionless at the water surface waiting for its prey and even when disturbed soon returns to the surface. Corixids are inactive at 0°C, but at higher temperatures collect detritus and algae and other food material from the bottom and after feeding in one spot move to another. Records of the number of moving insects at 5 second intervals, shows that in general the level of activity of a corixid population increases with the temperature. However, a rise in the activity of a few individuals tends to lead to the stimulation of the greater part of the group and the level of activity declines only slowly to its former low value. The activity level of corixid populations is, therefore, somewhat unstable. Predators such as *Naucoris cimicoides*, and Dysticidae are inactive at low temperatures but at higher temperatures are continuously on the move.

Efficiency of the Physical Gill. The volume of gas carried on the surface of a water bug or under the elytra of water beetles has been measured and the time the insects might be expected to remain submerged at various temperatures can be estimated from the known rates of oxygen consumption. The actual times of submergence in air saturated water has also been determined by direct observation upon inactive insects. The ratio of the observed to the expected periods of submergence at various temperatures for three water bugs are summarised in figure 1. In all the insects investigated, the metabolic rate, as indicated by the rate of oxygen consumption is negligible at 0°C, but gradually increases as the temperature is raised. Figure 1 shows that at temperature of 12°C or less the insects remain submerged for much longer periods than might be expected, showing that they augment their oxygen supply by using the surface gas stores as a physical gill. As the temperatures are increased the physical gills cease to function, at 15°C in *Notonecta glauca*, at 28°C in *Corixa punctata* and at between 35° and 40°C in *Naucoris cimicoides.*

Weather conditions in the British Isles. Average daily temperatures are at a minimum in February and at a maximum in August. Within this annual cycle, there are also diurnal cycles which are negligible in the winter months but in the summer can be large enough to be of great ecological importance. The British Isles are so situated that for the greater part of the year one depression after another crosses the country, though anticyclonic periods may occur in February, mid April to May, late August to mid September and in October or early November. In the spring and autumnal anticyclones, the temperatures of small bodies of water increase between dawn and mid-day, remain constant during the afternoon and then decline. As the temperatures increase, the insects become more active and the rate of oxygen consumption rises until a critical temperature is exceeded and the physical gill ceases to function. At the same time the insects surface more frequently and above the critical temperature become directly dependent upon the atmosphere for their oxygen supply and then tend to emigrate and fly to other habitats. Species which are ready migrants can be stimulated to fly during anti-cyclones by strong sunlight, especially if the dissolved oxygen tension of the water is low.

In small temporary habitats, the first insects to emigrate are small species like *Sigara nigrolineata* and *S. lateralis*, *Gyrinus natator*, and species of *Hydroporus*. Between 15° and 18°C *Hesperocorixa linnei*, *Callicorixa praeusta*, *Corixa punctata*, *Notonecta glauca* and *Acilius sulcatus* take

to the wing. In general the small species tend to emigrate before the larger species, but this appears to be correlated not so much with the temperature at which the physical gill ceases to function, but rather with the minimum temperature at which the energy output of the flight muscles is sufficient to lift the insect into the air.

Temporary habitats are subject to greater diurnal temperature variations than are permanent ones and as inhabitants of the former are also ready migrants, they tend to migrate during the late spring or summer to more permanent bodies of water and to return in the late autumn and/or early spring.

Differences in Migratory Behaviour. Young (1961) has shown that corixids which are reared at high temperatures develop wing muscles and become migrants, whereas members of the same species reared at lower temperatures in permanent habitats, have the flight muscles degenerate in the last nymphal instar and adults incapable of flight. Within the Corixidae, there is a wide range of migratory behaviour from species such as *S. nigrolineata* and *S. lateralis*, which are ready migrants and occur in temporary habitats, to species such as *Arctocorisa germari*, which live in permanent bodies of water and seldom, if ever, migrate.

The presence of wings in the denizens of the temporary habitats has an obvious survival value in as much as it enables the insects to emigrate to more permanent habitats when the temporary pools dry out in summer. The degeneration of the flight muscles in aquatic Hemiptera and Coleoptera living in permanent bodies of water gives three advantages: (1) the loss of flight muscles helps to reduce the rate of oxygen consumption and thereby increases the efficiency of the physical gills; (2) in *Naucoris* the space formerly occupied by the flight muscles is converted into air sacs and the volume of gas circulated through the physical gill is augmented; (3) these adaptations extend the range of temperatures at which the insects can remain submerged, and thus colonise permanent aquatic habitats where the critical temperature of the physical gill is rarely exceeded.

Conclusion. It will be seen, therefore, that the level of activity of submerged Hemiptera and Coleoptera as well as the migratory flight periods are correlated with changes in the efficiency of the physical gill due to annual, seasonal and diurnal variations in the temperature of the habitat.

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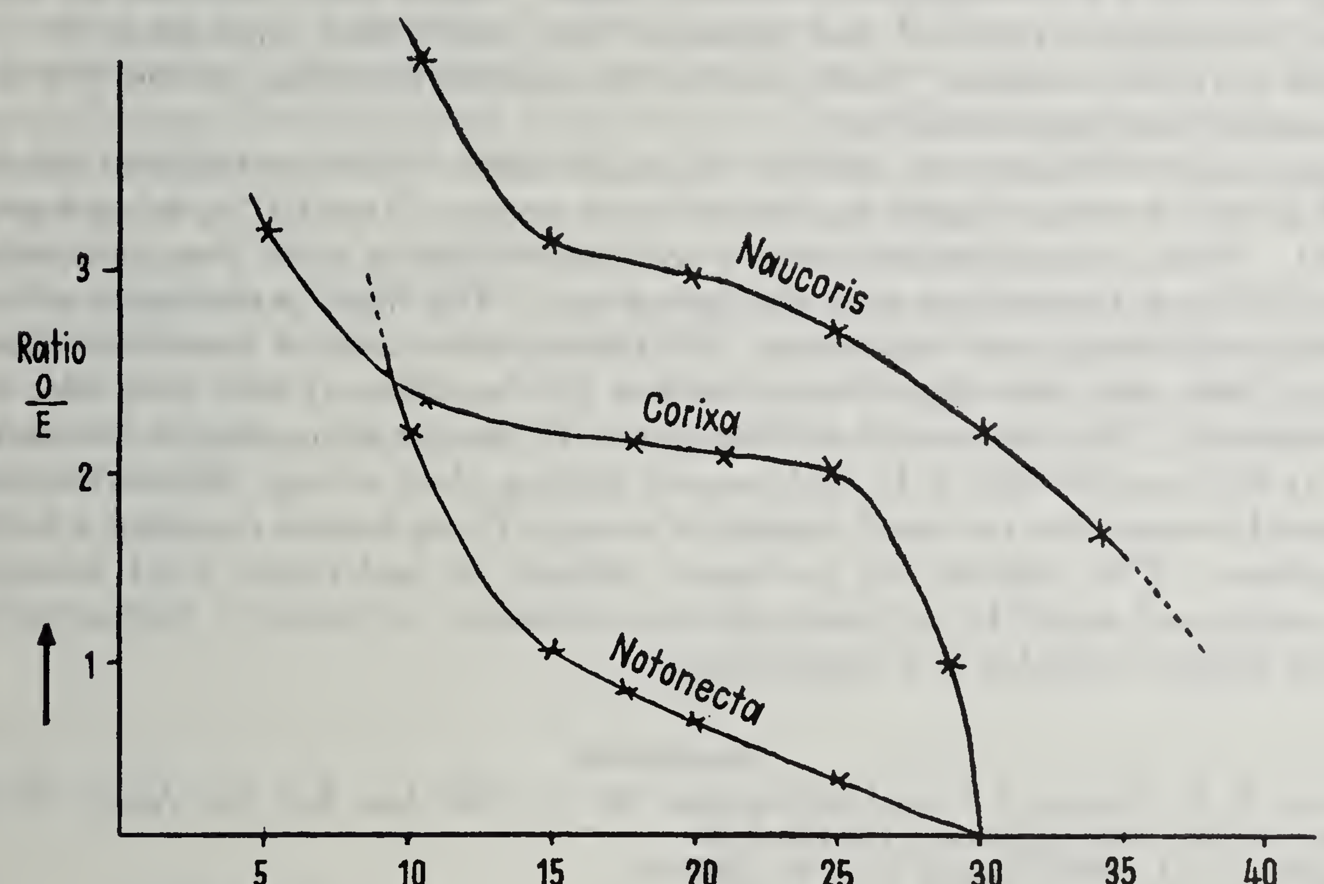

Fig. 1. Comparison of the ratio of the observed/expected periods of submergence of *Naucoris cimicoides*, *Corixa punctata* and *Notonecta glauca* over temperatures ranging from 0-35°C.

INDIVIDUAL VARIATION AND THE DISPERSIVE CAPACITY OF *NEODIPRION SERTIFER* (HYMENOPTERA)

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Southwood (6) has interpreted the whole phenomenon of migration as being related to the instability of habitats. In environments which fluctuate in size, a continuous dispersive activity involving less than the whole population may be a selective advantage. There appear to be a number of mechanisms by which a variable and limited flux of dispersing insects can be maintained, and in this paper there is preliminary evidence that yet another sort of mechanism also has this effect.

Neodiprion sertifer (Geoff.) overwinters in the egg stage; the larvae emerge in early spring and feed gregariously on the previous year's foliage. There are four or five larval instars; the prepupae are active wanderers; adults emerge in the height of summer, mate on the foliage and deposit their eggs. The species is found throughout N.E. North America, its host of preference being *Pinus resinosa.*

N. sertifer shows a wide range of behavioural capacity within a single population. The nature of this variation is far from completely known. The hatch of each batch of eggs takes place over a period of two days, with the earliest emerging larvae all apparently able to establish themselves on feeding sites; those emerging later always associate themselves with established larvae. The nature of these differences is not known.

There are thus major differences between individual larvae from the time of emergence from the egg, and as the larvae develop these differences persist. The individual rearing time to prepupa of "ex-first biter" larvae averaged five days faster than in mass colonial rearings. It is in the adults that the most interesting variation is found, however.

Frequent reports that females are poor fliers are common (3), although the males are strong fliers. The rather remarkable dispersive performance of *N. sertifer* which is known to infest very isolated plantings of its host does not seem to be explained by this account of female behaviour. There is no suggestion that long range dispersal of any larval form takes place.

Since males are known to be strong fliers, they were used to validate the experimental technique used in the investigation of female flight. Insects were mounted on flight mills and their performance recorded and translated into mechanical equivalents (5) and into equivalent free flight capacity. Males could fly the equivalent of 3 km. without rest and about ten times as far with intermittent rest.

A large series of females was tested by the same means. The vast majority either did not fly at all or only flew short flights equivalent to 1-5 meters. About 3-5% in each group flew very well! These unusual females could fly equivalent flights of up to 3 km. without rest and up to 15 km. with intermittent rests during the day. The flight performance of females is independent of mating and oviposition. No females flew until at least three hours after emergence, after that, their flight behaviour was fully established; none flew after five days from emergence. The extreme life of females was 12 days at saturation, in the dark and at 10°C. At 20°C and 40-60% R.H. with normal lighting, their average life was five days.

I would propose that the small number of strongly flying females represent a behavioural polymorphism. This explains the previously difficult to understand local infestations in isolated stands and would be of strong selective advantage in making a fluctuating and discontinuous habitat available to a population.

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DISPERSAL AND ITS SEASONAL VARIATION IN ROCK POOL CORIXIDS (HETEROPTERA, CORIXIDAE)

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An attempt has been made to study dispersal in *Corixa carinata* and *Corixa producta*, two species inhabiting temporary fresh-water pools of the southern archipelago of Finland. The pools of the area studied are generally one to three metres wide and less than half a meter deep and have no vegetation. The species occur in no other habitat in southern Finland.

Adults of both species overwinter and adults of the second generation appear in June. They rapidly attain maturity, and until the end of August the bulk of the population consists of mature individuals. Then adults appear which do not attain maturity until the following spring, and in October the population consists entirely of these overwintering adults.

Adults were marked with dots of cellulose paint applied to the ventral surface of the abdomen. The mark lasted well and did not seem to disturb the animals. The handling of individuals tended to induce flight immediately after release, however.

Elimination of marked individuals from the pools where they were released was mainly due to dispersal. The rate of elimination increased considerably during the season. The mean daily elimination for *C. carinata* was 10% in June, 15% in July, and 20% in August; for *C. producta* 15% in June, and 20-30% in July-August, respectively. This increase in later months was mainly due to exceptionally strong dispersal during the first few days after release. A daily elimination of 40% was often observed, which indicates the existence of exceptionally mobile individuals in the population. These are probably immature adults, whilst the mature individuals, on the contrary, are assumed to retain their characteristic mobility throughout the season.

Recoveries outside the places of release indicated that dispersal was random. In the study area, comprising more than 200 pools, the mean distance from the place of release calculated from recoveries during successive five-day periods was 30-100 metres in June, but later the more mobile immature individuals increased it to 230 metres for the first five-day period in both species. For subsequent periods values of 60-130 metres were obtained, which indicates that the more mobile individuals rapidly dispersed beyond the study area.

In October, the adult population became concentrated in the pools that were sufficiently deep for overwintering. This aggregation is accomplished by random mobility combined with less frequent dispersal from deep pools than from those too shallow for overwintering. By the time that low temperature inhibits dispersal in late autumn, most individuals are aggregated in deep pools and those left in other places are eliminated during the winter. Repopulation of shallow pools occurs in May, after sexual maturation is completed.

The results indicate a distinct difference in mobility between immature and mature adults. Mature individuals are mainly confined to limited areas, and this ensures efficient use of all temporary breeding places. The mobility of immature individuals, on the other hand, has clear migratorial features. The present method, however, is unsuitable for studying long-range movements of corixids.

THE DISPERSAL FLIGHT OF *MELIGETHES* BEETLES AND SPRING MIGRATION OF DELPHACIDS WITH SPECIAL REFERENCE TO THE APPLICATION OF THE TRACER METHOD

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The use of radioisotopes as tracers represents an important advance in insect migration and dispersal studies. From the data obtained we can see the limitations of this method in the physical qualities of the r-isotope and the effectiveness of the checking method on the one hand and in the restrictions imposed by the medical regulations on the other.

This method was first used in Czechoslovakia for work on the ecology of the leafhopper *Javesella pellucida* Fabr., the vector of oats sterile dwarf virus, to study its migration from hibernation to spring oats. Other experiments were carried out with bees to test their effectiveness in visiting alfalfa flowers and with *Meligethes* beetles visiting rape flowers.

Method. We used the water isotope solution of $Na_2HP^{32}O_4$ or $NaH_2P^{32}O_4$ of spec. activity 50-150 μC/ml to render plant sap r-active. In 24 hours the leafhopper r-activity was 100-1000 counts/min. This secures a sufficient detection by autoradiography of recaptured material up to 4 weeks after release. Pollinators were marked by feeding on honey and sugar paste to which was added water mixed with $H_3P^{32}O_4$ with spec. activity 50 μC/ml. *Meligethes* beetles were marked by the dipping method. Water solution $H_3P^{32}O_4$ with the spec. r-activity 11·7 μC/ml was used for 4 min. The detection of r-active specimens after 8 days' exposure was secured by gluing them on a safety pack Röntgen film. In this way we can find differences measuring only 5 counts per minute.

Field experiments. In the first experiment 1,200 specimens *Javesella pellucida* F. were marked. The growth of oats and the nearly ended migration did not permit sweeping a larger sample; in 2 checks 630 specimens at weekly intervals were obtained. Only one r-active female was found in the oat field where the marked material was released and one male specimen at a distance of about 500m to the south east. The following year about 17,000 speciments were marked, released at their place of hibernation and checked at successive weekly intervals. 5,572 specimens were swept but only 8 were r-active. The maximum distance of migration from the point of release was 824m to the south east (the prevailing wind direction). The marked material had evidently spread over an area exceeding 2-3 km in diameter, because no strikingly higher number of r-active specimens was found in fields closest to the point of release.

The marking of pollinators of alfalfa was negative in the fields during all the six days of investigations.

The marked 138,000 *Meligethes* spp. predominantly *M. aeneus* F. were released on 27.5.1964 at a spot some metres distance from the flowering rape. The speed of flight of the beetles was 150m per hour. 85 samples swept after 1, 50 and 98 hours contained 465 r-active specimens out of 131,300, showing the dispersal to be nearly regular over the area. This experiment was repeated and 483,000 specimens were marked, in a different area, near a wood in the centre of some distant fields of rape. In the nearest field (200m away), r-active material was found 2 hours after release and on the following day we swept r-active material in all three fields within a circle of one km in diameter. The samples obtained showed an average of 26 r-active specimens in 15,000 beetles checked. After 8 days, at a distance of about 4·3 km an average of 10 specimens were obtained in similar samples.

All these experiments go to show that the radius of action and mobility of flying insects is much higher than previously supposed, so that the actual maximum distance of migration can hardly be ascertained either by means of a portable detection apparatus or by sweeping.

MOVEMENTS OF SOME INSECTS TO AND INSIDE RAPE FIELDS

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For a proper understanding of the influence of the distribution and rotation of crops on the population density and the degree of attack of various agricultural insect pests there is a need for increased knowledge about the mode of spread of the latter. There are reasons to suspect that a comparatively slight adjustment of the crop production in many cases would result in less damage with decreased demands for chemical control.

In order to get data of the movements of some phytophagous insects and their hymenopterous parasites to and within rape fields large-scale studies were started in 1962 at the National Swedish Institute for Plant Protection. The main interest in these studies is devoted to the Brassica Pod Midge (*Dasyneura brassicae* Winn.) and the Bladder Pod Weevil (*Ceuthorrhynchus assimilis* Payk.) of which particularly the former is a serious pest of rape in Sweden. As found by many investigators the midge is largely dependent on the weevil in using for egg-laying the punctures in the pods made by the latter. Curiously enough the midge itself seldom if ever succeeds in piercing the pod wall. In studying the spread of the midge this relationship between the two insects has to be taken into consideration.

For the investigations the sweeping method has been extensively used. It is true that several objections can be made against this method in synecological work but for studying the distribution of separate insect species and their movements in more or less homogeneous habitats, e.g. in many crops, the method is often convenient. As shown by the present studies this is valid for the Blossom Beetle (*Meligethes aeneus* F.), the Brassica Pod Midge and the Bladder Pod Weevil in rape fields.

In 1962 sweepings were made before and especially during the flowering period in a large number of fixed places in three rape fields, and later in the same year the extent of midge attack in different parts of these fields was thoroughly determined. Counts of the pods damaged by the midge were in 1962-1963 carried out also in many other fields. Moreover, in studying the spread of the midge the tagging technique with radioactive phosphorus (P^{32}) was successfully tested and used in a field experiment in 1963. Another more extensive tagging experiment is now (summer of 1964) under way.

To sum up some of the results it seems appropriate to point out first that the weevil often concentrates at the border parts of the winter rape field early in the season but later disperses more or less evenly over the whole field. This agrees with observations made by Bonnemaison (*Ann. Epiphyt.*, 8 (4), 1957, p. 418) in France. The attacks by the larvae of the midge on winter rape generally become much more serious along the edges than elsewhere in the field, and this seems largely to be due to the particular behaviour of the midge. Thus, this latter insect shows a distinct tendency to congregate along the edges, and frequently this happens also when the weevil for weeks has been observed as occurring abundantly over the whole field. The studies clearly indicate that the special micrometeorological conditions prevailing at the borders do not constitute the only reason at least for the congregation of midges there. They also present strong evidence that the invading midges congregate at once after their arrival at the field, i.e. without moving at first through the rape area.

The location of the winter rape fields in relation to the previous year's rape areas influences the occurrence less markedly in the case of the weevil than in the case of the midge. It seems evident that this at least to a large extent is connected with differences in the hibernation habits between the two species.

FACTORS INFLUENCING DISPERSAL OF INSECTS IN RAINFOREST AREAS CONVERTED TO CACAO LANDS

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More than 220 insects were found associated with cacao as a host plant in the Territory of Papua and New Guinea (2 and 3). Only eleven of these are considered as major pests. These are: Miridae: *Pseudodoniella laensis* Miller, *P. pacifica* China and Carvalho, *P. typica* (China and Carvalho). Coreidae: *Amblypelta theobromae* Brown. Noctuidae: *Achaea janata* L., *Tiracola plagiata* (Wlk.). Lamiidae: *Glenea aluensis* Gah., *G. lefebueri* Guér. Curculionidae: *Pantorhytes plutus* Oberth., *P. proximus* Faust., *P. szentivanyi* Msl.

It was observed in three cacao growing areas of Papua and New Guinea that species of the weevil genus *Pantorhytes* invade cacao plantations some years earlier than those of the Mirid genus *Pseudodoniella*. It is believed that this phenomenon is connected with the different nature of the host plants of *Pantorhytes* and of *Pseudodoniella*. The main indigenous host plant of the three *Pantorhytes* species is the relatively small urticaceous tree *Pipturus argenteus* which is one of the plants present in the natural rainforest. However, on clearing the forest, *Pipturus* becomes the dominant regrowth species. Subsequently there is an invasion of *Pantorhytes* populations on to the *Pipturus*, growing almost as a weed in areas prepared for cacao planting.

The host plants of the *Pseudodoniella* species are various species of *Ficus* which as a rule do not appear in clearings or in secondary forest. When the tall forest trees (including *Ficus*) are felled, the *Pseudodoniella* spp. lose their source of food (the fruit of *Ficus*) and at this initial stage of plantation establishment their populations move from the cleared area into the rainforest.

The reason for the appearance of the *Pseudodoniella* species at a later stage in the cacao plantations is probably the result of complex factors which need further study. One of the explanations could be the following: as more and more land is cleared for cacao planting, the mirid population of the area loses more and more of its natural habitat (rainforest) and local food shortages eventuate. It is known that relatively small numbers of Odoniellini mirids are able to cause severe damage to a large number of cacao trees. This was observed in the case of *Pseudodoniella typica* in New Britain (1) and of *Pseudodoniella laensis* on the New Guinea Mainland. Williams observed in Ghana that because of the destructiveness of feeding habits of *Sahlbergella singularis* and *Distantiella theobroma* a number of nymphs died of starvation (5). An intraspecific competition occurs at times in the populations of African mirids (4). This probably occurs to an even larger degree in the *Pseudodoniella* populations after having lost much of their natural habitat. This brings about the mass invasion by adults of *Pseudodoniella* of the areas which they had to evacuate on clearing. The next step is their adaptation to *Theobroma cacao* as a host plant.

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HIBERNATION UND GREGARISATION VON HEUSCHRECKENSCHWÄRMEN IN ARGENTINIEN

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Die Bildung von Heuschreckenschwärmen im südamerikanischen Gregarisationszentrum findet nur in einigen wenigen Wüstengegenden unserer Republik statt. Eine dieser Flächen, La Antigua (8000Km^2) liegt südlich der Provinzialhauptstadt La Rioja und eine andere, El Milagro (2000Km^2) westlich der genannten Lokalität. Alles situiert in einer Tiefebene (300-120 m Seehöhe) in Kesselform im N., NO, W und SW von Hochgebirgszügen umschlossen und bekannt als "Llanos de La Rioja".

Es ist ein Trockengebiet, teils wüstenähnlich (Ariditätsfaktor (0·00-0·22), Fast vegetationslos ausser psammophilem Buschwerk und spärlichen niedern Bäumen; Der Boden der Dünen überzieht sich alljährlich nach Regen mit einer niederen Saisonflora, deren Entwicklungsgrad und Dichte von der jeweiligen Regenmenge abhängt. So werden die Dünen geeignet zur Eiablage und nachherigen Entwicklung der Heuschrecken, die zugleich mit den Regenwinden die Zone erreichen und dort ihre Fortpflanzung beginnen.

Die Heuschreckenhüpfer die sich dann unter günstigen Bedingungen in grösseren Mengen entwickeln, verlassen allmählig ihren Entwicklungsraum wegen des Schwindens ihrer Nährpflanzen durch Frass und Vertrocknung. Während dieser Flucht- und Suchbewegungen vereinigen sich immer mehr Brut-Gemeinschaften zu Schwärmen, welche schliesslich bei ihren Ausbruchsaktionen als Flugtiere hauptsächlich nach N. und NO. geführt werden im Einklang mit den lokalen, dominanten Windrichtungen. Weiter im N. begegnet diese Flugbewegung dauernden Gegenwinden von fast konstant gleichmässiger Frequenz welche den Ausbruch der Flugschwärme aus dem zitierten Kessel verhindern, Winde die nur während sehr kurzer Zeit durch aufsteigende Nachmittags-Thermalströmungen aufgehoben werden.

Solche Aszendenz warmer Luft lässt die Insekten in höhere Luftschichten gelangen und dort Gegenwinden folgen, die aus dem genannten Kessel hinausführen, aus der Ursprungszone und den Brutplätzen heraus in die Kulturzonen. Die Flüge innerhalb der warmen Luftmassen dauern bis diese durch Difusion mit der umgebenden Kaltluft sich derselben angleicht.

Zum Fliegen benötigt unsere *Schistocerca cancellata* Serv. eine Körpertemperatur von 23°C. die ab April nicht oft verfügbar ist, wenn die Bodenwärme nicht benützt werden kann. Die Bedeutung der herrschenden Aussentemperaturen ersieht man aus nachstehenden Beobachtungen: (aufgenommen in La Guardia, Telaritos, San Martin, Flughafen La Rioja (Unergrund T.); Höhenwerte vom Flugzeug und Helikopter aus.)

Temperaturen, La Rioja

Monat	*Mittel*	*Max.* 120*cm.*	*Min.* 120*cm.*	*Max.* 20*cm.*	*Min.* 20*cm.*	– 10*cm.* *Untergrund*	– 20*cm.* *Untergrund*	– 30*cm.* *Untergrund*	50/100*m* *Höhe*
April	20·6	28	–9	36	0	16·4	22·2	22·6	14
Mai	13·8	23	–5	29	–5	11·7	15·5	18·3	11
Juni	11·8	19	–4	28	–4	9·3	14·2	14·6	6
Juli	8·5	11	–3	28	–2	6·6	11·1	11·4	7
August	13·9	18	0	30	0	9·3	14·1	14·1	10

Nach dem Einsetzen der kühleren Zeit verbringen die Heuschrecken die Nacht (bis—9°C) in Bodennähe oder am Boden selbst wo sich Anhäufungen und Massen sammeln. Die Wärmeausstrahlung des Bodens und Untergrundes (16—22°C) beschleunigt die morgendliche Steigerung den Insekteninnentemperatur; die weitere Erhöhung der erdnahen Luft auf 30° leitet dann den Flug ein, der anfangs nur als lokale Evolution aufzufassen ist, den über den Wipfeln herrscht erst in den Nachmittagsstunden Flugtemperatur. Diese sinkt rasch mit abnehmender Höhe und zwar im Beispielsfalle, auf 14°C, was für den Schwarm Flugunfähigkeit bedingt. Die erkälteten Tiere müssen landen um nach einer neuerlichen weiteren Erwärmung wieder flugfähig zu werden.

Sobald sich diese Prozesse im benachbarten, unregelmässig bewaldeten Gebirgshang abspielen, erzeugt die Verschiedenheit der ökologischen Faktoren und dementsprechenden Belichtungsverhältnissen grosse Unterschiede in der Erwärmungszeit und folglichen Beweglichkeit der Tiere, was weiterhin zu einer fortgesetzten progressiven Aufteilung der Wintermasse führt.

Die notwendigen, günstigen Faktorenkombinationen für grössere Flüge kommen während der Herbst- und Wintersaison nicht oft vor, weswegen grosse Mengen von Heuschrecken massiert im genannten Waldgebiet der Sierra Ancasti halb verborgen blieben, und sich erst ab Vorfrühling fortbewegen und langsam verteilen, bis sie nur mehr kleinere Gemeinschaften bilden, die dauernd weiter zerfallen um endlich als solitäre Individuen unauffällig werden.

EVOLUTIONARY IMPLICATIONS OF BEHAVIOUR

EVOLUTION OF ACOUSTICAL BEHAVIOUR IN THE PHANEROPTERINAE (ORTHOPTERA, TETTIGONIIDAE)

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Most sound-producing Orthoptera have the same general system of long-range acoustic communication. The solitary males of each species have a single type of movement of the stridulatory apparatus. Each such movement produces a characteristic sound, the *phoneme*, which is the unit of structure for the spontaneous song of that species. This phoneme is produced in some particular rhythm to form the species-specific song. The sexually responsive females are attracted to the songs of the males of their species and do not make functional sounds themselves.

Study of 24 species of phaneropterines in eastern United States by Mr. John D. Spooner and myself has revealed that their long-range acoustic communication differs from the general pattern among Orthoptera in these respects: (1) solitary males of some species produce two, three, or four distinctive phonemes, (2) solitary males of some species produce two, or even three, distinctive spontaneous songs, (3) a single spontaneous song may combine as many as four phonemes in a stereotyped pattern, (4) the sexually responsive females produce ticking sounds in response to spontaneous songs of the males, and the males move toward the females by using these ticks for orientation.

In 6 of the 24 species, males produce a single phoneme and a single spontaneous song.

In 12 species the solitary males produce two phonemes. In five of these the two phonemes are produced independently, resulting in two simple spontaneous songs. In two species the two phonemes are always produced in the same stereotyped pattern resulting in a single complex spontaneous song. In the remaining four species the two phonemes are sometimes but not always produced in a predictable pattern.

Four species are known in which the solitary males produce three phonemes. In two of these each phoneme is used in a separate spontaneous song, i.e. there are three spontaneous songs. In the other two species two of the phonemes are always produced in a stereotyped pattern so that each of the species has one simple and one complex spontaneous song.

Two species produce four phonemes, and in both these species all four are produced in a stereotyped pattern resulting in a single (highly) complex solitary song.

The simple spontaneous songs of phaneropterines may be classified according to function as follows: (1) female-attracting song (hereafter, FA), (2) female-tick-eliciting song (FTE), and (3) male-spacing song (MS). No simple spontaneous song has yet proved to combine any two of these functions. On the other hand complex spontaneous songs sometimes combine two (or perhaps all three) of the functions listed. Experiments with electronically reproduced complete and incomplete songs have shown that (1) one phoneme of a complex song may be completely responsible for a particular function of the song, (2) two or more phonemes of a complex song may be required in combination to be optimally effective in a particular function, (3) the response to a song may change with the song's intensity.

The evolution of the various systems of phaneropterine acoustic communication is most easily explained by postulating a common ancestor with two simple spontaneous songs, FA and FTE. The FA is primitive in ensiferan Orthoptera, and the FTE most likely evolved from an alternation of sounds during courtship, which in turn had evolved from incidental sounds made by the female in her responses to a distinctive courtship song of the male.

From a common ancestor with FA and FTE, all known modern systems could have evolved by various combinations of the following changes: (1) FA lost, (2) sequence of phonemes becomes stereotyped, (3) function of one phoneme of a complex song spreads to other phonemes of the same song, (4) male spacing sound develops from sounds made by males in contact with one another, (5) female-attracting function of a complex song lost, (6) new female-attracting phonemes develops from sounds made by males in response to the female tick. Each of these changes is possible by means of a series of individually adaptive steps, and many of these intermediate steps are illustrated by modern species.

THE PHYLOGENETIC DEVELOPMENT OF FOOD SELECTION IN ORTHOPTERA (*SENS. LAT.*)

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Various authors have noted the late Tertiary appearance of extensive grasslands in North America and the rapid evolution of the modern horse are related events. Few appreciate that similar correlations are obtainable from among Orthoptera. The fact that they are is indicated by certain palaeoentomological conclusions viewed in light of food selection in extant forms.

The first orthopteran food-habit was omnivory, and perhaps emphasised eating of dead plant and animal materials. This habit appeared in the Pennsylvanian in Blattoidea and probably in Protoblattoidea and Protorthoptera. Possible foods to which these archaic insects had access included several kinds of plants (algae, fungi, mosses, liverworts, ferns, seed ferns, horsetails, club mosses, conifers, cycads) and animals (various ancient insects, other arthropods, snails, amphibians). From omnivory among certain cockroaches there followed

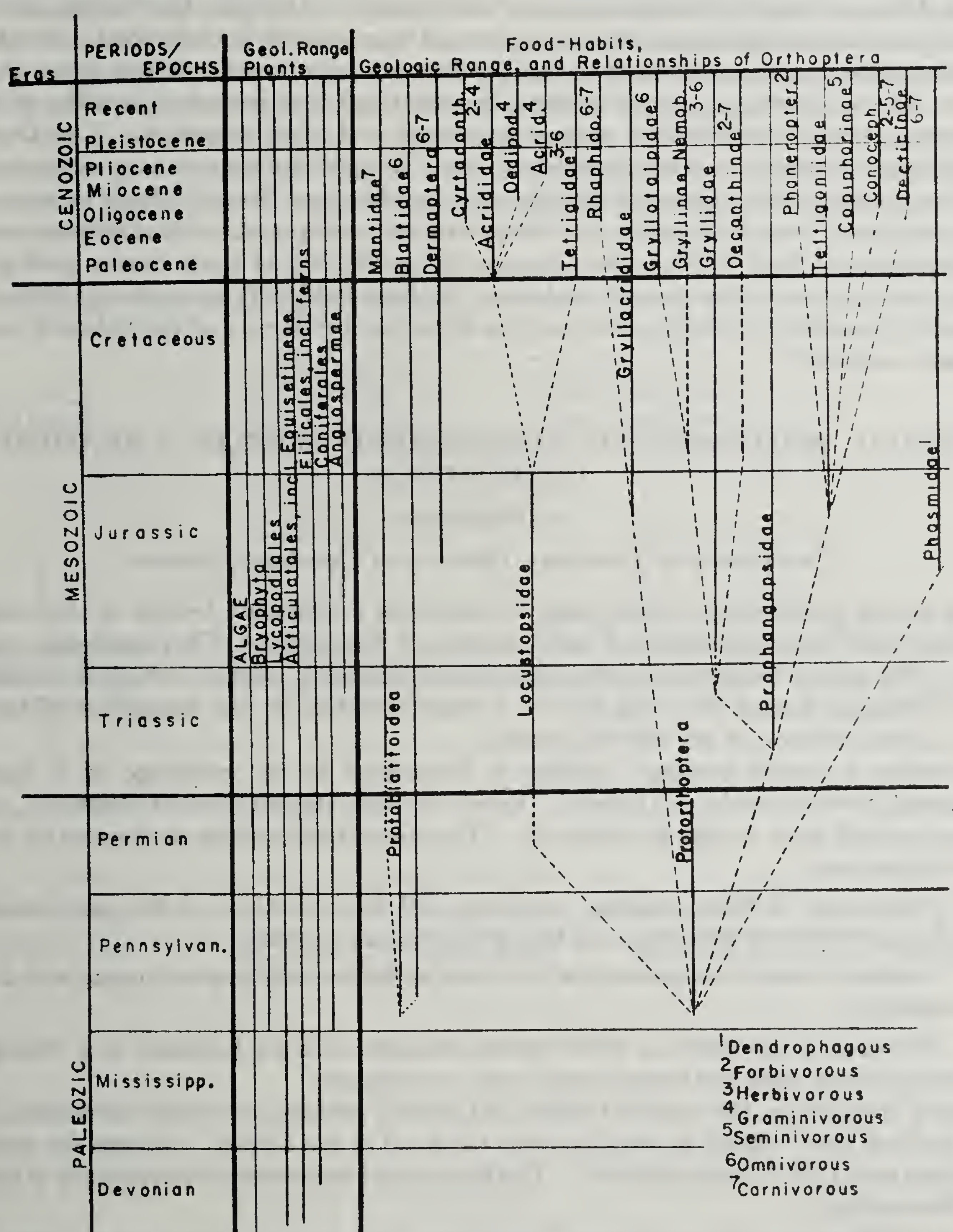

Fig. 1. Phylogenetic development of food selection in Orthoptera.

specialisation for predatism, a kind of carnivory, and led to the rise of Mantoidea. The appearance of mantids apparently correlates with the development of an extraordinarily diverse Permian insect fauna available as food. The above habits, carnivory and omnivory, constitute the ancestral patterns subsequently retained in a number of groups and modified in others as the development of new foods allowed.

The first major break with the omnivorous-carnivorous ancestral patterns occurred in the Jurassic, when woody dicots became widely available as food, making possible the rise of Phasmoidea. The second major departure occurred during the Miocene and Pliocene, when herbaceous monocots and dicots became abundant, and open grasslands replaced the widespread forests of earlier times. Several new groups of Orthoptera appeared and adopted forbivorous, graminivorous, or related habits. The rise of Phaneropterinae appears to be associated with the development of dicots. Certain ancestral katydids probably retained carnivorous tendencies, but others became wholly phytophagous on the leaves and flowers of dicots, especially herbs. The ascent of Conocephalinae, Copiphorinae, and particularly Acrididae is closely associated with changes in the occurrence of grasses. The first known Acrididae appeared in the Palaeocene, but the group may not have flourished until the Oligocene and Miocene, when grasslands became widespread. Acridids, like horses, are characteristically organisms of plains and savannah, bound to grasslands both for food and habitation.

Other modern groups appeared in the Tertiary and continued to follow either the omnivorous or the carnivorous ancestral pattern, but modified it to include quantities of the new plant (monocot and dicot) and/or animal (mammal and bird) materials. The Decticinae, Listroscelinae, Saginae, various Gryllidae, and Rhaphidophorinae are examples. The Tetrigidae, a group of omnivores, is notable in its emphasis on "lower" plants as items of diet.

In conclusion, most food-habits in Orthoptera are widespread, occurring in several of the major phylogenetic lines of the order; changes in availability of foods during geologic times were important factors in the group's evolution; the food-habits of many recent subfamilies are comparatively modern, extending back only as far as the Tertiary; and the habits of others are exceedingly ancient.

THE SEXUAL BEHAVIOUR OF LONGHORNED BEETLES (CERAMBYCIDAE: COLEOPTERA)

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The sexual behaviour of more than 30 species of longhorned beetles of the subfamilies Lepturinae and Cerambycinae and some species of Donaciinae (Chrysomelidae) has been studied. The sexual behaviour of these animals represents a complex which is suited for the study of releasing factors and also, due to a large variation in the behaviour of the recent species, of the evolution of stimulatory actions.

Courtship is almost lacking. Mating is dominated by an exchange of a number of tactile stimuli between male and female. Except for the establishment of amplexus, chemical and visual stimuli seem to play a minor role. The stimulatory actions performed by the males may be divided into:

1. *Oral actions*: licking, tapping, scraping, and biting actions of the male mouthparts upon the female elytra or pronotum, or biting of a female antenna.

2. *Abdominal actions*: movements of the male abdomen and genital organ, and a pulling of the ovipositor.

3. *Movements of legs*: striking of the female abdomen with the hindlegs, or a wiping action of the foremost tarsi upon the female head, eyes, or antennae.

During stimulation the males of almost all species perform antennal movements (which may be divided into 7 types) in the air above the head of the female. Except for one species these strokes never hit the female body. The function of the antennal movements is uncertain (visual stimulation?).

As a rule the stimulatory actions are rhythmical, and normally when two or more of these actions are combined they are synchronised, the same pattern of synchronisation being found

in different species. In a few species, however, some actions may be non-rhythmical or non-synchronous compared with other actions. When actions are combined the relative intensity of the components may vary considerably.

The synchronisation between licking actions, tapping actions, and abdominal movements, suggests some sort of a coupling between the spatially separated parts of the CNS primarily responsible for the individual actions.

The licking action is simple, almost identical with the movements of the palps seen during feeding. It occurs in morphologically primitive species and, combined with other actions, in almost all species. If the licking action is considered the original type of stimulation, it is possible to derive most of the more complex types from the licking by *gradual* changes in behaviour, also when new effector systems are introduced (see figure).

I think that during the evolution new actions performed by the same or another effector system have been introduced *continuously*, beginning as weak movements coupled synchronously to the original action. The new action may then grow more violent, gain a signal value, and perhaps lose its synchronisation with the original action, which may then become lost. Most of the intermediate steps postulated have been found in the behaviour of recent species.

Similarly, in these animals it is possible to understand the stridulation sounds as a consequence of a *continuous* evolution from the incidental "background music" caused by the stimulatory tapping action. Considering the great role of tactile stimuli in the sexual behaviour of insects, a similar evolution might have occurred in other groups too.

The evolution of the behaviour outlined here agrees reasonably well with the systematic grouping of the species. In addition to the intersexual behaviour violent fights between the males of some Cerambycinae and various releasing factors have been studied and will be published elsewhere.

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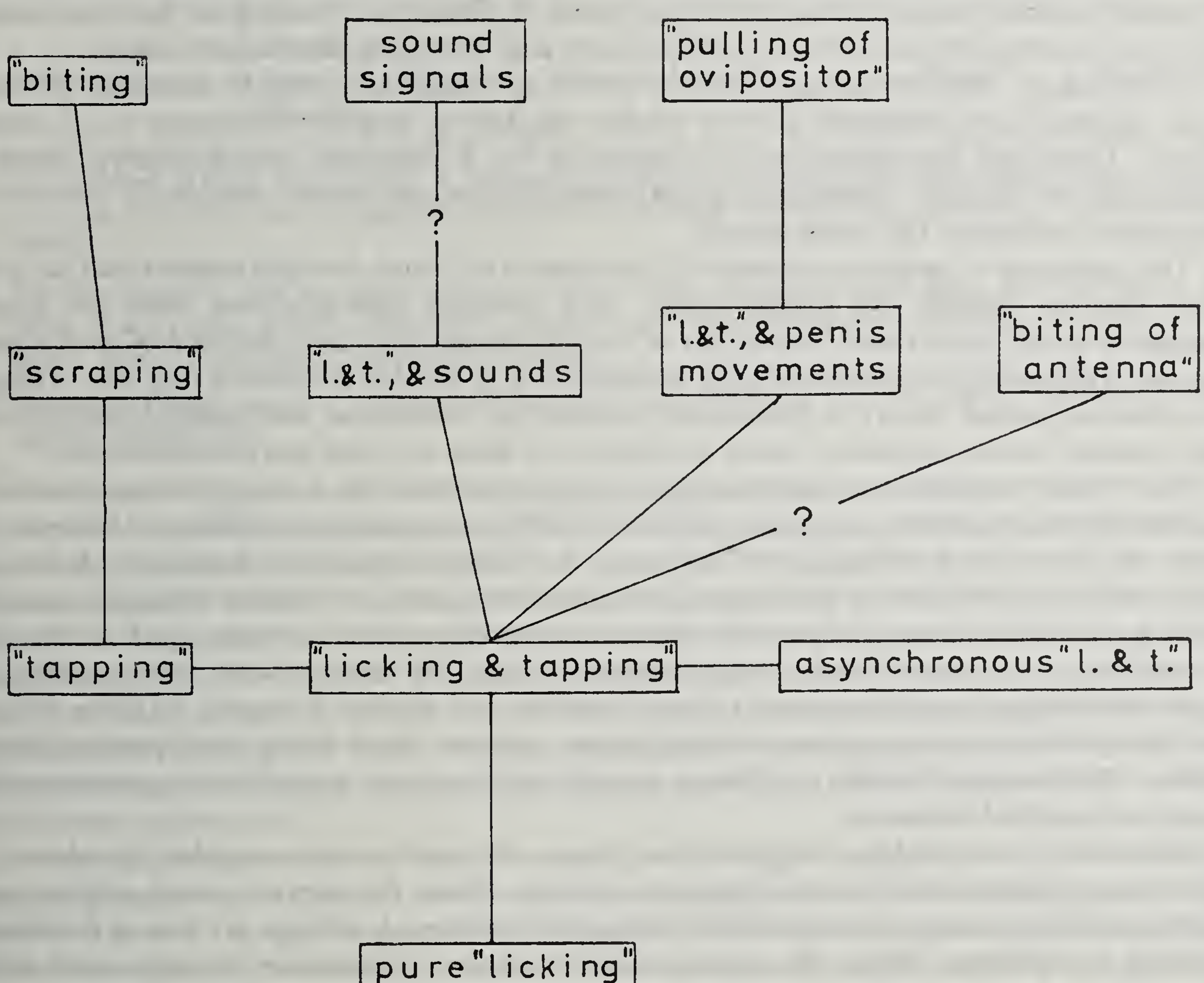

Fig. 1. Derivation of complex types of behaviour from licking.

LEARNING AND INSTINCT IN INSECTS

CYCLIC FUNCTIONS IN GENERA OF LEGIONARY ANTS (SUBFAMILY DORYLINAE)*

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The nomadism which characterises all doryline ants is cyclic and is based upon reproductive conditions in the colonies.

The genera *Eciton*, *Neivamyrmex* and *Aenictus*, termed *group A* by virtue of their regular nomadic-statary cycles, are contrasted here with the genera *Dorylus*, *Anomma*, *Labidus* and *Nomamyrmex*, termed *group B* by virtue of their variable nomadism.

Group A is represented by the tropical American species, *Eciton hamatum*, the cyclic behaviour of which involves the regular alternation of (1) nomadic phases of 16-17 days in which surface bivouacs are open, large daily raids lead into nightly emigrations, and the queen is contracted throughout, with (2) statary phases of 20-21 days in which the bivouac site is enclosed, raids are small or sometimes absent, emigrations are rare, and the queen lays a large batch of eggs midway in the phase.

A set of correspondences arising consistently between colony behavior and brood conditions in surface-adapted *Eciton* species and in *Neivamyrmex nigrescens* (Schneirla, J. Comp. Psychol., 1938; Ins. Soc., 1958) involves: (1) the presence of a brood of mature and enclosing pupae as each nomadic phase begins, (2) completion of the larval stage by a new all-worker brood during each nomadic phase, and (3) pupation of this brood in the next statary phase, when the queen delivers a new batch of eggs. Evidence on the Old World genus *Aenictus* (Schneirla and Reyes, in prep.) discloses conditions similar to these.

Evidence for group A supports my theory of tactual and chemotactic stimulation from the brood initiating, maintaining and ending the phases of the colony nomadic-statary cycle. The pupal-eclosion factor initiates nomadic phases in *Eciton* and *Neivamyrmex* but is secondary in *Aenictus*, in which the larval factor both initiates and maintains the nomadic phase.

Evolutionary affinities among group A genera are suggested, both by nomadic phases of similar duration and causation and by similar egg-laying episodes of queens in all species studied. Divergent specialisations are suggested by a distinctly longer statary phase in *Aenictus* and by *Aenictus* producing quasi-monomorphic all-worker broods in contrast to polymorphic broods in the other genera.

The regularity of ovulation episodes in the queens of group A might suggest that an endogenous rhythm controls the colony cycle. But evidence indicates that both the regular physogastry in the queen and facilitation of oöcyte development near the end of each statary phase are attributable to brood-induced stimulative and trophic conditions (fig. 1). Hence a *colony-situation-feedback* theory is formulated postulating stimulative and trophic interrelationships between worker segments, brood and queen as basic to cyclic doryline functions.

This theory explains the continuation of cyclic functions in group A when seasonally-conditioned sexual broods are produced, also clarifies an important difference between the broods of *Aenictus* and other genera in group A. The polymorphic broods of *Eciton* and *Neivamyrmex* are attributed to two factors postulated for queen and colony situations, namely: (1) the later oöcytes come in the series, the more ovisorption they undergo, and (2) the later any member of the brood reaches each successive stage, the more it loses in stimulative and trophic advantages dependent upon colony situation and worker behavior. Of the oöcytes, those losing least in these respects produce major workers, those losing most produce minim workers. Polymorphic broods contribute greatly to behavioral specialisation, monomorphic broods to simplified behavior.

For *Aenictus*, our findings suggest three factors as basic to monomorphic broods and to longer statary phases than in other group-A genera. First, the oöcytes are *all* subject to far more loss through ovisorption than in the other genera; second, all eggs are low in stimulative attraction for workers; third, the workers are relatively unresponsive through most of the statary phase when a condition approaching dormancy prevails among them. The result may

* Supported by National Science Foundation

be that the eggs (or embryos) of potential all-worker broods in *Aenictus* retain a state resembling aestivation until a major change in the colony improves stimulative and trophic conditions affecting them. Such a change must occur in the last week of the statary phase, when maturation and eclosion of the pupal brood arouses the workers to action. This brood then enters the microlarval condition with individual differences at a minimum. Although monomorphic population conditions in *Aenictus* oppose specialisation in the organisation of behavior, cyclic functions are as regular and efficient as in group-A genera with polymorphic populations.

Table I

Cyclic Functions in Doryline Ants

Generic Groups	*Area*	*Cyclic function Type*	*Phases*	*S-factors in cycle*	*Queen's egg-laying*	*Worker populations*
A. Epigaeic spp. of *Eciton*	New World	Regular	N - S^1	*Callow* and *Larval*	On - off; regular	Polymorphic
Neivamyrmex	New World	Regular	N - S	*Callow* and *Larval*	On - off; regular	Polymorphic
Aenictus	Old World	Regular	N - S	*Larval* (& callow ?)	On - off; regular	*Monomorphic*
B. Others *Dorylus* and *Anomma*[2]	Old World	Irregular	Variable[3]	*Callow* (& larval)	Continuous ? —irregular peaks	Polymorphic
Labidus	New World	Ditto ?	Ditto ?	Ditto ?	Ditto ?	Polymorphic
Nomamyrmex	New World	Ditto ?	Ditto ?	Ditto ?	Ditto ?	Polymorphic

(1) The phases of each cycle are: *N*, a *nomadic* interval of large daily raids and emigrations and *S*, a *statary* interval of no emigrations and low raiding activity (Schneirla: J. Comp. Psychol., 1938).

(2) Postulations for *Dorylus* and *Anomma* based upon Raignier and Van Boven (1955, Ann. Mus. Roy. Cong. Belge), those for *Labidus* and *Nomamyrmex* upon preliminary observations of my own (1957, Proc. Amer. Phil. Soc.).

(3) Group-B cycles involve isolated emigrations in alternation with statary phases of highly variable duration.

Findings of Raignier and Van Boven on *Anomma* and *Dorylus*, with observations of my own on species of *Labidus* and *Nomamyrmex* (Table 1; figure 1), suggest that group-B nomadism, in contrast, is confined to single emigrations occurring at variable intervals. By the colony-situation-feedback theory I have advanced, under group-B conditions only the callow-stimulative factor can normally raise the colonies to the metabolic and excitatory level of emigrating. The basis may be (1) a much wider range of brood-stimulative conditions due to the commonly greater heterogeneity of their broods, (2) a lower brood-worker communicative efficiency in their much larger colonies, and (3) physical and physiological factors deterring communicative processes in the less organised, more diffuse subterranean bivouacs of these genera than in group A.

As cyclic patterns evolved in doryline ants, natural selection presumably weighted factors promoting synchronous changes in stimulative and trophic interrelationships between workers, brood and queen. Such factors evidently advanced well in group-A genera with their relatively small colonies and surface adaptations, but not in group-B genera with their large colonies operating from subterranean bivouacs.

On morphological grounds, Emery termed *Aenictus* an "archaic" doryline. The same

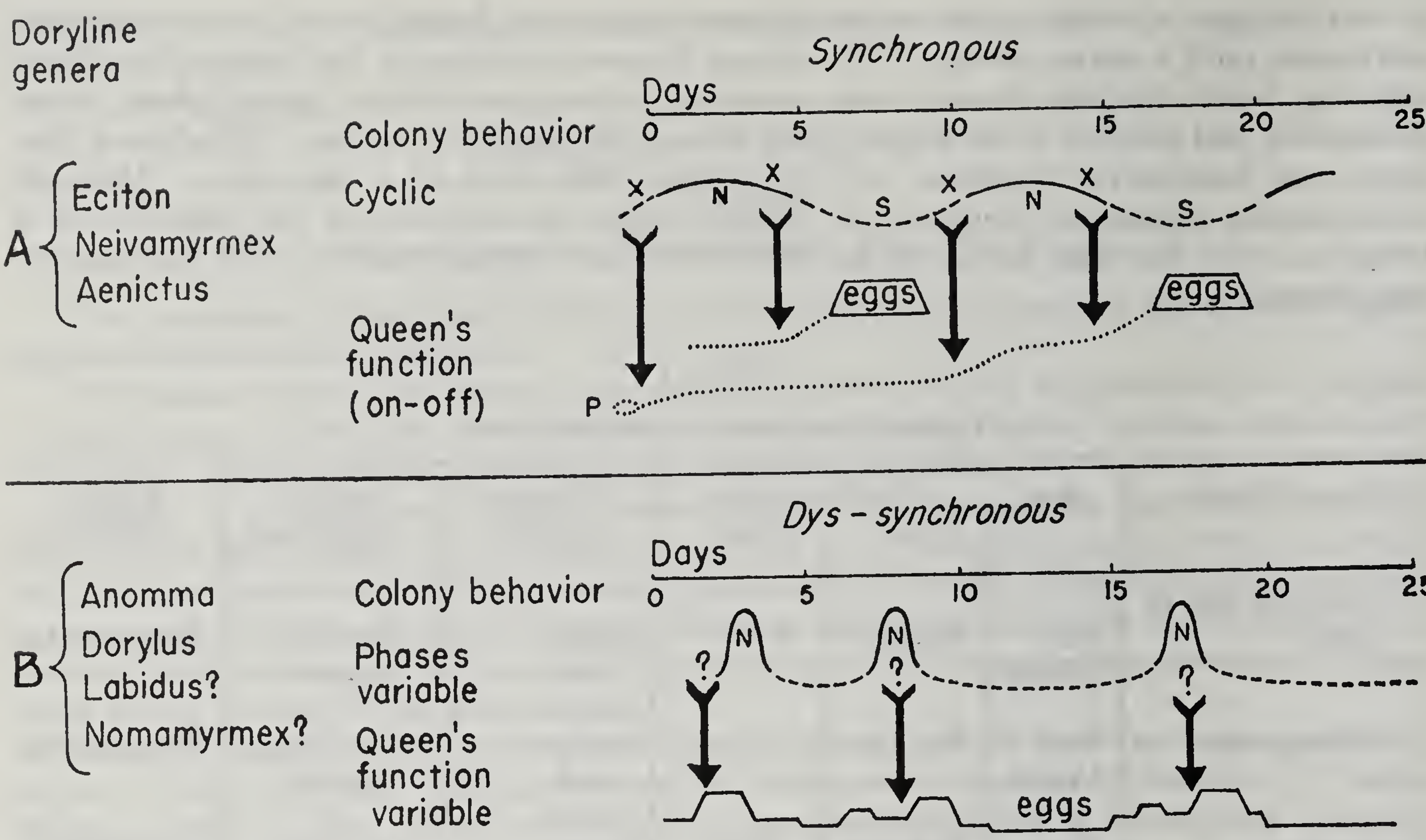

FIG. 1. Schema of generic differences represented in Table 1, in which sources are noted. (Explanation in text).

term is available for *Aenictus* colony behaviour in that the simple surface bivouacs and abbreviated, quickly transformed raids in this genus may resemble primitive conditions in the hypothetical doryline ancestry although contrasting sharply with the complex organised group functions of epigaeic *Eciton* species. Even so, in the regularity and efficiency of its cyclic functions, *Aenictus* matches the other group-A genera in specialisation.

In contrast, group-B genera, while retaining a basis for nomadic colony behaviour, evidently diverged in the direction of more variable cyclic operations carried out by greater populations always from subterranean bivouacs.

SUR CADRES CYLINDRIQUES ET SPHERIQUES, LES ABEILLES MODIFIENT LEUR ARCHITECTURE

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Les cellules hexagonales construites sur cadres droits figurent le prisme régulier. Sur cadres cylindriques, de telles cellules ne peuvent s'adapter; les Abeilles modifient leur construction et créent la forme de pyramide tronquée.

Constatations: les cellules de la face extérieure du cylindre s'élargissent suivant un double apothème horizontal et se retrécissent, à l'intérieur du cylindre, suivant le même plan et cela de la base vers l'orifice.

Données: pour un cylindre de 100 mm de diamètre, l'ensemble de 10 cellules extérieures ainsi élargies, mesure 78 mm; pour l'intérieur, ces 10 cellules rétrécies mesurent 48 mm; différence 30 mm. Au départ 10 cellules sur cire gaufrée mesurent 60 mm/. L'angle de 60° resultant normalement de la rencontre de deux apothèmes sur câtés contigus supérieurs, passe à 75° pour les cellules extérieures et à 45° pour les cellules intérieures.

La construction sphérique entraine la modification de l'inclinaison des 6 côtés de la cellule. En épousant la sphère, les cellules occupant des positions différentes, passent de 0° à 90°.

ANALYSE DE LA TRANSMISSION DES DIVERS PARAMETRES DES SIGNAUX ACOUSTIQUES CHEZ LES HYBRIDES INTERSPECIFIQUES DE GRILLONS (ORTHOPTERES, ENSIFERES)

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Le problème de la transmission héréditaire des signaux acoustiques est étudié chez les Grillons par le biais de croisements interspécifiques. Les divers paramètres morphologiques des émissions sonores des espèces parentes (P1, P2), des hybrides réciproques de première génération (F1) et des rétrocroisements (F1 × P1 ou P2), sont comparés (seuls ceux concernant la fréquence sont consignés dans le tableau ci-dessous). Quatre espèces, interfécondes deux à deux, sont à l'origine des populations hybrides analysées: il s'agit d'une part de *Teleogryllus commodus* Walk. et *T. oceanicus* Le Guillou d'Australie dont les signaux sonores sont émis selon un rythme complexe, et d'autre part de *Gryllus argentinus* Sauss. et *G. peruviensis* Sauss. d'Amérique du Sud, aux émissions acoustiques plus simples.

Les résultats, bien que différents, sont similaires pour les deux séries d'expériences; ils mettent en évidence les faits suivants:

1. Les caractères morphologiques des signaux acoustiques sont identiques pour tous les hybrides de première génération (F1) et ce, quelque soit le sens du croisement. Pour aucun des paramètres des signaux acoustiques (fréquence, composition et durée du motif) on n'observe de dominance, tous sont intermédiaires à ceux des espèces parentes (P1 ou P2).

2. Les hybrides de rétrocroisements (F1 × P1 ou P2) ont une stridulation propre; les différents paramètres de leur émission sont intermédiaires à ceux de l'espèce parente (P1 ou P2) utilisée en retour et à ceux de la F1. Aucune disjonction n'apparait.

3. De nombreux gènes, répartis sur divers autosomes, participent selon toute vraisemblance à la réalisation des divers paramètres des signaux acoustiques comme à celle des appareils de stridulation.

4. Les appréciations quantitatives des divers paramètres des signaux sonores des espèces (P1 et P2) et des différents hybrides (F1), (F1 × P1 ou P2), peuvent s'ordonner selon le pourcentage supposé d'autosomes issus respectivement des deux parents (classification des rétrocroisements en fonction de l'association des autosomes spécifiques: G. Cousin 1955).

5. Les signaux sonores étant innés et contrôlés par les centres nerveux, on est amené à considérer que les nouvelles combinaisons chromosomiques déterminent une structure topographique originale ou un fonctionnement nouveau des centres nerveux chez les hybrides dont les signaux sonores inédits ne sont que les reflets.

6. Chaque catégorie d'hybrides ou d'espèces possèdent des signaux acoustiques bien caractérisés. Il n'est pas interdit de penser que dans la compétition sexuelle la rencontre des sexes et les accouplements ont d'autant plus de chance de se réaliser que les signaux acoustiques se ressemblent, chaque population d'hybrides tendant ainsi à s'isoler. On entrevoit là un mécanisme possible de différenciation spécifique.

TABLEAU. Fréquence en kHz enregistrement à 25°C ± 1

	parent P1	*P1 × F1*	*F1*	*P2 × F1*	*parent P2*
commodus → oceanicus	3,5	3,8	4,1	4,7	4,8
peruviensis → argentinus	3,2	—	3,4	3,8	4,1
% autosomes P1	4/4	1/4	1/2	1/4	0
% autosomes P2	0	1/4	1/2	3/4	4/4

BEWEISE DER FÄHIGKEIT DER INSEKTEN DEN KREIS, DAS DREIECK UND ANDERE EINFACHEN FIGUREN ZU UNTERSCHEIDEN

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Es gilt die Behauptung, daß die Insekten, z.B. die Bienen, nicht imstande sind, die einfachen geometrischen Figuren voneinander zu unterscheiden, dagegen aber vermögen sie die mehr komplizierten Figuren zu unterscheiden.

Hertz (1933, 1934) und später Autrum (1948, 1957) entwickelten die Ideen von Exner (1891), indem sie die Wahrnehmungen der Form bei den Insekten mit ihren eigenen Bewegungen in Zusammenhang gestellt hatten, wann die grafischen Eigenschaften der Gegenstände nur als bestimmte Reihenfolge von Flimmerscheinen wahrgenommen werden.

Und wenn man die Wahrnehmungen der Form nur also Behalten von bestimmter Reihenfolge der Flimmerscheine betrachtet, dann müssen die Insekten tatsächlich die komplizierten Figuren ganz leicht zu unterscheiden vermögen, dagegen aber soll das Unterscheiden von einfachen Figuren voneinander für die Insekten schwerfallen.

Ob die Bienen in den Versuchen von Hertz (1929) nur wegen der Unfähigkeit, die Form zu unterscheiden, den Kreis, das Kreuz und das Dreieck verwechselt haben? Sie hat zwei große dunkle Figuren, z.B. den Kreis (5,5 cm Durchmesser) und das der Fläche nach gleiche Dreieck, auf einen hellen Hintergrund gelegt.

Aber die Insekten wegen des kurzen Abstandes von den Figuren die Umrisse dieser relativ großen Figuren nicht sehen könnten: die Figuren projezierten sich auf solche Weise, daß es unmöglich war, derer Umrisse zu erkennen. Wenn die Insekten den Köder unmittelbar über den Figuren suchten, darüber flogen oder sogar sich darüber bewegten, so wurde sowohl der Kreis, als auch das Dreieck für die Bienen tatsächlich zu den gleichen dunklen Feldern mit unklaren Umrissen in der Peripherie.

Wir benutzten in unseren Versuchen mit den Bienen zusammengesetzte Figuren, derer Umrisse für die Insekten nicht nur vom Abstand, sondern auch in der Nähe sichtbar waren, wenn die Bienen sich unmittelbar auf der Figur befanden. Jede solche Figur wurde aus mehreren gleichen Figuren zusammengelegt: die größte Figur bestand aus einigen kleineren Figuren der zweiten und der dritten Klasse. Damit die Wahl von dem Ausmaß unabhängig war, wurde eine von den zu vergleichenden Figuren gleichzeitig durch 5 nach der Größe unterschiedliche Muster (von 1,2 bis 2mal) dargestellt und die andere, wo der Köder untergebracht worden war, wurde im Laufe des Versuches mehrmals durch ännliche, größere oder kleinere, ersetzt. Die Fläche der Figuren der ersten Klasse betrug 25-30 cm^2 und die der dritten—3,3 bis 7 mm^2.

Die Berechnung der Zuflügen von markierten Bienen zu verschiedenen Figuren hat gezeigt, daß die Bienen fähig sind, die Figuren (Kreis, Dreieck, Quadrat) zu unterscheiden und daß diese Aufgabe für sie anscheinend nicht schwerfällt, ebenfalls nicht schwerer, als den Mehr-Strahlen-Stern von einer nicht gegliederten Figur, z.B. vom Kreis, zu unterscheiden. In beiden Fällen war das Prozent von fehlhaften Wahlen im Laufe des fünfstündigen Versuches unbedeutend gering und praktisch gleich ($\sim$15).

Die mißlungenen Versuche von früheren Autoren mit der "Belehrung" der Bienen, die einfachen Figuren zu unterscheiden, erklärt sich also in Wirklichkeit dadurch, daß sie zu große Figuren verwendet haben (wie auch in den Versuchen von Hertz).

Die Insekten vermögen die einfachen Figuren zu unterscheiden (nach ihren Formen), es schließt aber die Möglichkeit nicht aus, daß die Insekten die zergliederten Figuren (Objekte) in der Bewegung auch nach der Reihenfolge der von ihnen erzeugten Flimmerscheine erkennen könnten.

DEVELOPPEMENT DU COMPORTEMENT DE FILAGE DE LA SOIE CHEZ UNE ESPECE DE TRICHOPTERE: *MOLANNA ANGUSTATA* CURT

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L'origine des mouvements de filage a été recherchée dès la période embryonnaire de l'animal. L'embryon présente essentiellement des mouvements dissymétriques qui tendent à dérouler ou à enrouler son corps. Parmi les premiers, certains tendent à relever la tête de l'embryon. Le processus de l'éclosion (percement du chorion par le *ruptor ovi*, que porte la tête, et dégagement de l'animal de ses enveloppes embryonnaires) est assuré par le jeu des mouvements alternatifs de déroulement et d'enroulement du corps.

Au cours des trente premières heures de sa vie, la larve demeure dans sa ponte gélatineuse. C'est alors qu'apparaissent la pigmentation et le durcissement du tégument larvaire. Il se produit également une augmentation du tonus musculaire, qui se traduit par le télescopage des segments abdominaux et par l'accélération des contractions musculaires. Les mouvements caractéristiques du comportement embryonnaire se répètent de temps à autre; de plus, de nouveaux mouvements se manifestent. Mais, pour la question qui nous intéresse ici, nous retiendrons surtout:

—en premier lieu, qu'à partir des premiers mouvements de déroulement et d'enroulement, nous voyons apparaître des mouvements de redressement complet du corps et des mouvements plus ou moins amples d'incurvation du corps, symétriques ou dissymétriques. Les uns et les autres alternent fréquement;

—en second lieu, que les mouvements dissymétriques de la tête s'amplifient et, bientôt, se répètent d'une manière soutenue, en changeant alternativement de sens. La tête se balance alors de droite à gauche et de gauche à droite. Pendant ces mouvements, le labium, à l'extrémité duquel s'ouvre la filière, demeure souvent protracté.

Les précédents mouvements du corps et de la tête interviennent lors du filage de la soie.

Le comportement de filage, quand l'animal édifie la paroi de son fourreau. Lorsque l'animal édifie la première partie de son fourreau, il relie sommairement les éléments entre eux à l'aide de deux ou trois fils de soie, posés au hasard. Les mouvements de la tête sont assez amples.

Quand l'animal édifie les parties successives de son fourreau, il relie de plus en plus étroitement les éléments entre eux, par des fils de soie très serrés. Les mouvements de balancement de la tête deviennent alors de plus en plus précis.

Le comportement de filage, quand l'animal forme le revêtement soyeux sur la face interne de la paroi du fourreau. Le tapissage intérieur est réalisé au cours de plusieurs périodes de filage. Le dépôt de soie n'intéresse parfois qu'une courte zone de la partie antérieure du fourreau. On remarque alors surtout les mouvements de balancement de la tête. Mais l'animal peut aussi poser de la soie sur toute la moitié antérieure du fourreau. Il présente alors un ample mouvement d'incurvation du corps et s'enfonce dans son fourreau; puis, tandis qu'il se redresse, il pose la soie, toujours à l'aide des mouvements de la tête.

Discussion, Conclusions. Cette étude montre l'analogie entre le comportement de filage des Trichoptères et celui des Lépidoptères (décrit par Van der Kloot, W. et Williams, C. en 1953). Les mouvements de balancement de la tête de la larve de *Molanna* sont analogues à ceux de la chenille de *Platysamia cecropia* (swing-swing). De même, les mouvements d'extension et d'incurvation du corps sont semblables à ceux des chenilles (stretch-bend). Nous montrons en outre que ces mouvements apparaissent très tôt et dérivent de ceux de l'embryon.

Cette étude souligne également que les mouvements de filage deviennent de plus en plus précis au fur et à mesure de la construction du fourreau. Nous pensons que c'est l'état du fourreau qui exerce une action directrice sur le comportement de l'animal.

SUR LA CONSTRUCTION DE LA TOILE DE *ZYGIELLA X-NOTATA* CL. (ARAIGNEES, ARGIOPIDAE)

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Nous étudions trois situations différentes en plaçant tour à tour un cornet de papier faisant fonction de retraite contenant l'araignée aux coins d'un cadre hexagonal à base horizontale. Nous constatons que le moyeu de la toile suit les déplacements de la retraite, entraînant des variations dans la répartition et la longueur des rayons.

Nous avons mis en évidence une corrélation, vérifiée statistiquement, entre le nombre de rayons des régions "supérieure et inférieure" délimitées par une horizontale passant par le moyeu. Deux facteurs agissent sur cette répartition:

(1) La position de la retraite qui augmente le nombre de rayons dans la région opposée;

(2) Le pesanteur qui l'augmente toujours sous le moyeu.

Ces deux actions sont synergiques dans la toile habituelle.

L'inégale longueur des rayons entrainée par la situation de la retraite et la forme du cadre détermine la forme de l'éllipse (Il existe une corrélation pour toutes les sortes de toiles, entre la longueur des rayons et la distance de la spire captrice la plus externe).

Cette corrélation reste valable au cours de la croissance et fait penser à une influence de la longueur des pattes sur les dimensions de la toile.

Les spires sont moins espacées à la partie inférieure quels que soient l'excentrement et la position de la retraite. Il semble que cette différence soit due au poids de l'abdomen qui, en haut de la toile, tend à ramener les filières vers les pattes alors qu'en bas il les en éloigne, L'araignée ayant toujours l'abdomen vers l'extérieur de la toile.

Variations au Cours de la Croissance

Il y a augmentation de la surface captrice et du nombre de spires, le nombre de rayons augmente de l'éclosion à l'adulte mais diminue chez l'adulte. Les caractéristiques de la toile ne varient pas aprés la ponte qui fait perdre plus de la moitié du poids de l'araignée. Celui-ci n'intervient donc pas directement sur les caractéristiques de la toile. La hauteur s'accroît plus que la largeur de la surface captrice en relation avec une plus grande augmentation de la longeur des rayons verticaux. Le seul facteur d'augmentation des dimènsions n'est pas la longeur des pattes.

Esquisse d'une Explication de la Toile

Après la pose des rayons, tous n'ont pas la même tension, au moyeu seulement, la résultante de toutes les tensions est nulle, mais chaque rayon a sa propre tension. Les spires provisoires et définitives sont posées en fonction de ces tensions et de l'écartement entre les pattes. D'autres recherches préciseront cette hypothèse.

CONTRIBUTED PAPERS

BIOLOGY OF A SLUG-KILLING FLY, *TETANOCERA ELATA* (DIPTERA: SCIOMYZIDAE)

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A summary of the biological investigations of 84 species of snail-killing Sciomyzid flies was presented at the Eleventh International Congress (1). The total number of species reared is now over 100, and the recent discovery that several species feed obligatorily on slugs expands knowledge of the broad and complex ecological radiation which has occurred within this family. Information concerning invertebrate enemies of slugs, as many aspects of the biology of slugs, is mostly fragmentary and inconclusive. *Tetanocera elata* Meigen apparently is the first insect known to feed exclusively on slugs. Two North American Sciomyzidae (3) and an additional European species have also been discovered to be host specific to slugs.

All Sciomyzid larvae reared to date kill and feed only on aquatic and terrestrial pulmonate Gastropoda. Snails and slugs belonging to eighteen families are known to be attacked in nature; several more families have served as hosts and prey in laboratory rearings. Sciomyzid larvae exhibit a wide range of feeding behaviour. At one extreme, there are many aquatic, predaceous species that kill quickly, each larva destroying as many as 23 snails (e.g. *Elgiva* spp. 4). At the other, there are a few terrestrial, parasitoid species, each larva of which kills only one snail during its development (e.g. 2). Between these two extreme modes of behaviour there are many species with intermediate and mixed habits, some having more predaceous (5), others more parasitoid tendencies (e.g. *Tetanocera elata*). Correlated with the type of feeding habits are differences in other behavioural features, such as sites of oviposition and pupation, host specifity, and seasonal aspects.

Tetanocera elata is widely distributed in Northern and Central Europe and may be locally abundant in moist, shaded areas of dense herbaceous vegetation. In the laboratory *elata* females mated readily and each laid up to 373 eggs. First instar larvae remained motionless near the empty egg-membranes and kept the anterior two-thirds of the body uplifted. The host slugs, *Agriolimax* (=*Deroceras*) *reticulatus* (Müll.) and *A. laevis* (Müll), were infested as they crawled past the larvae. The air-breathing larvae penetrated under the mantle until only the posterior spiracles remained exposed. They fed on mucus, without killing the slugs, throughout the first instar and during part of the second. In later life they behaved as predators, killing each of a series of 4-9 slugs quickly, feeding at the anterior end for a short time, and leaving each victim as soon as satiated. Larvae were not host specific during the predaceous stages, but killed and ate *Arion fasciatus* (Nils.), *A. intermedius* (Norm.), *Limax flavus* (L.), *L. tenellus* (Müll.), *Milax budapestensis* (Haz.), and *M. sowerbyi* (Fér.). Mature larvae were placed with *Arion ater* (L.), *A. hortensis* (Fér.), and *A. subfuscus* (Drap.) but did not attack them. At 19-24°C a complete life cycle required 61-90 days: preoviposition period, 13; incubation period, 7-9; first larval instar, 4-10; second larval instar, 8-15; third larval instar, 15-23; and pupal period, 19-20 days (except for overwintering pupae). During a five month period of activity two generations may be produced, and a third may develop to the overwintering pupal stage.

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LABORATORY EXPERIMENTS ON THE SPONTANEOUS TAKE-OFF ACTIVITY OF *BLASTOPHAGUS PINIPERDA* (COL., SCOLYTIDAE) IN RELATION TO TEMPERATURE AND LIGHT INTENSITY AT DIFFERENT SEASONS OF THE YEAR

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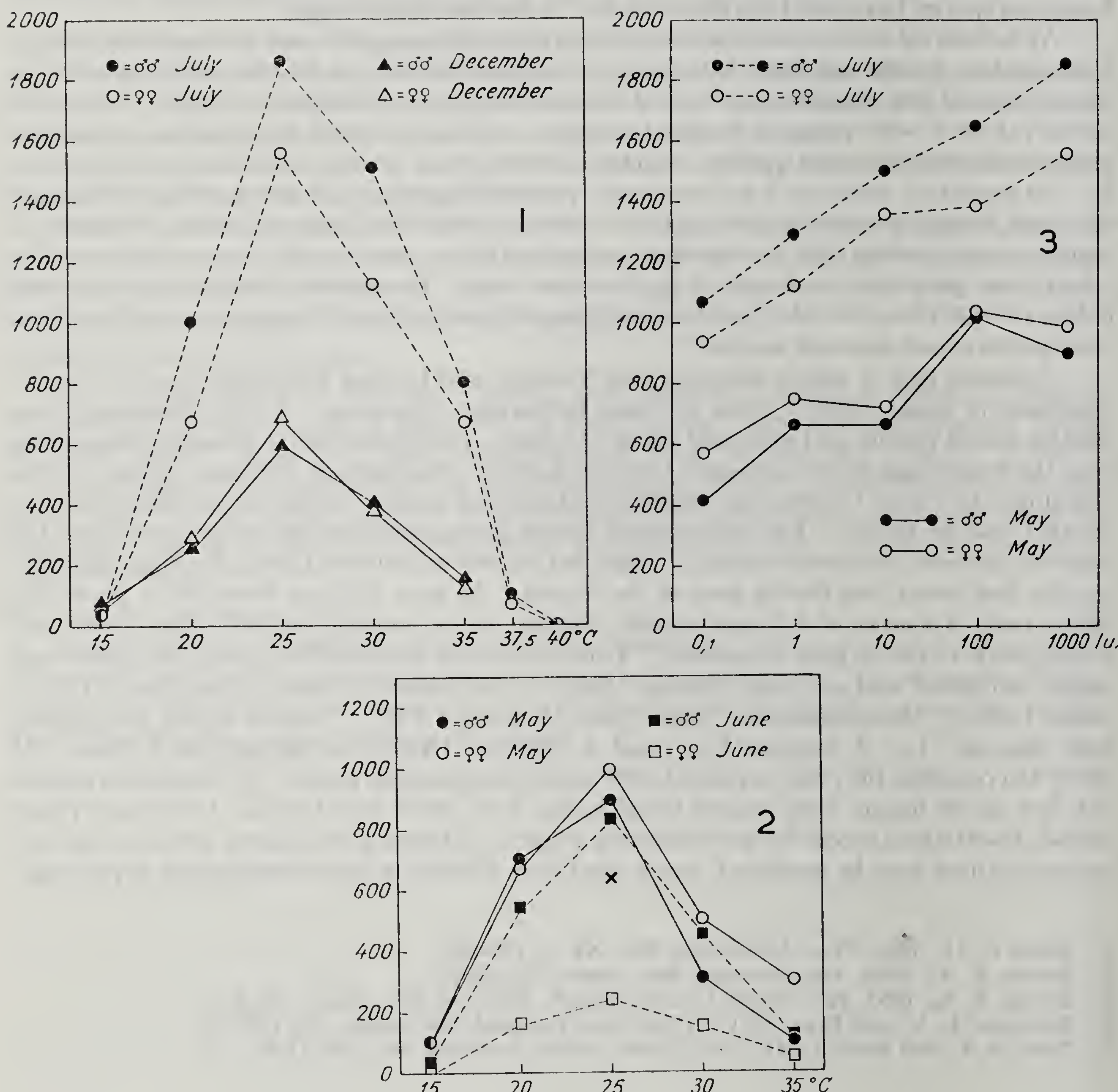
The take-off activity of *Blastophagus piniperda* was studied in constant laboratory conditions (see legends to figures). The pre-adaptation of the beetles to light, temperature and humidity was always the same.

When studied at intervals of 5°C., the take-off rate in all seasons (figs. 1 and 2) was very low at 15°, much higher at 20°, and maximal at 25°C.; at higher temperatures it gradually decreased.



FIGS. 1-3. (1) Effect of temperature on the take-off rate of *Blastophagus* in July and during hibernation; each point represents the total number of take-offs in ten 15 min. experiments (100 specimens); air humidity 77% R.H., light intensity 1000 lux (Perttunen 1958); ordinate: number of take-offs; abscissa: temperature in °C. (2) Effect of temperature on the take-off rate in the swarming and egg-laying seasons and in the females after egg-laying (X, see text). (3) Effect of light intensity on the take-off rate at 25°C and 77% R.H.

But at each given temperature marked seasonal differences were also observed. In July the recently emerged specimens of the new generation showed the highest flight activity in the experiments (fig. 1). This high flight activity corresponds well to their behaviour in the forest at this time; they fly to the pine shoots in the crowns of the trees. They feed inside these shoots until autumn when they go to hibernate at the bases of pines well below the snow level in the winter. Taken from these hibernation places in November and December they still showed some flight activity in laboratory conditions, but the take-off rate was much reduced compared with July (fig. 1). In the spring the beetles leave their hibernation sites and fly to pine logs to lay eggs inside the bark. During this swarming period in May the take-off activity (fig. 2) in the laboratory conditions was higher than during the hibernation period, although clearly lower than in July. The females taken from their tunnels in the middle of their egg-laying period in early June showed an extremely reduced take-off activity, whereas the activity of males taken from the same tunnels at the same time was about as high as during the swarming period (fig. 2). Whether the very low take-off rate of the egg-laying females is due to a reduction of the wing muscles similar to that observed in other scolytids (1, 2, 3, 5) is not known. In any case, after the females had finished egg-laying, fed on bark for some time and were about to leave their galleries, they again showed a markedly increased take-off rate (fig. 2, marked X). By this time the males had already disappeared from the tunnels.

The take-off rate is also dependent on the light intensity (fig. 3), but even in the very dim light of 0·1 lux the flight activity was only reduced to about half the rate observed at 1000 lux. Since it was also observed that the take-off rates in dry (0% R.H.) and moist (100%) air did not differ greatly from the rates at 77% R.H. in the swarming period, it is evident that temperature is the most important of these three environmental factors in the initiation of flight.

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BIOLOGY AND BEHAVIOUR STUDIES IN A TEMPERATURE GRADIENT

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The thesis behind these studies is that the extensive investigations of *Tribolium* biology in uniform environments have been neglected insect behaviour, and may there provide an unreliable background to economic pest control.

The temperature gradient apparatus used in these studies was designed to provide a relatively large working area which would hold at least six gradient troughs at one time. The apparatus is undergoing radical modifications so details of construction are omitted. The temperature gradient was of a very even slope, and there were no differences between trough positions. A major feature was the temporal stability of the gradient which permitted the study of gradient biology over periods of several months. The apparatus provided a simulated natural environment; the troughs contained wheat-feed, and the temperature gradient was not separated from the concomitant humidity gradient.

A study of the life cycle of *Tribolium castaneum* in the gradient environment showed that the adults orientate on the gradient of temperature in a manner which determines their fecundity and the site of oviposition. Rather than saying that fecundity ranges from one egg per day at 21° to sixteen eggs per day at say 36°C., I was able to show that fecundity was about ten eggs per day over the range of 21°-36°, and the eggs are laid in a narrow zone around 29°.

Since the site of oviposition is precisely determined by adult orientation, the incubation period is predetermined.

Larvae start their development in the neighbourhood of 29°, yet the larval period is not that to be expected at a uniform 29°. The larvae orientate in the gradient environment as they develop, and behaviour and development become synthesised. The relative lengths of the larval instars are not as found in any C.T. room. The most interesting aspect of the larval gradient biology is a short visit by the larvae to temperatures near 35° just prior to pupation which occurs at a temperature of 30°-31°.

The selection of a specific temperature for pupation predetermines the length of the pupal period. The length of the pupal period is in fact slightly less than would be expected at a uniform temperature of 30.5°, and this is due to the visit by prepupal larvae to temperatures in the region of 35°. The preoviposition period is a uniform seven days as a consequence of the orientations of the teneral adults.

Comparisons have been made of the gradient biology of *T. castaneum* and T. *confusum.* The overall length of their cycles were in the region of 28 days and 40 days, respectively. In the so called optimal uniform environments the length of the life cycle of *T. castaneum* is 20 days, and for *T. confusum* it is 25 days.

Gradient biology studies not only bring an ecological reality to investigations of life histories, but also result in a questioning of the extrapolation of C.T. room data to problems of control techniques in the field. Another suspicion is that culturing at uniform temperatures places extreme selection pressures on laboratory populations; in the long term the C.T. room will produce an unrepresentative strain, and in the short term it may produce experimental groups with an unwanted high variability, e.g. the response to a fumigant may be more variable within a group cultured under the stress of a uniform environment. Also suspect is the ecological applicability of intraspecific and interspecific competition studies done in uniform environments.

POPULATION STUDIES ON THE CITRUS PURPLE SCALE, *LEPIDOSAPHES BECKII* NEWM. IN EGYPT

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The purple scale, *Lepidosaphes beckii* Newm. is a major destructive pest of citrus orchards in Egypt. The population dynamics of this pest and factors governing its distribution on citrus trees were studied in an orchard 20 years old that was never interfered with by any control measures.

The mean monthly temperature ranged in the two years of the study between a minimum of 7·8° and 6·7°C to a maximum of 30·3° and 32·6°C. The orchard is relatively humid and more rainy than other localities in Egypt. The microclimate of the insect was much the same as the macroclimate except that the surface temperature of the citrus leaves exposed to the sun was always above the air temperature.

The distribution of the population of the purple scale on the trees was governed by the following factors:

Variety of Citrus. This was studied by artificially infesting with nymphs 27 trees belonging to 8 citrus varieties 2 years old, and by sampling naturally infested citrus fruits and leaves from the orchard and then estimating the number of scales/fruit or leaf. The results indicated significant difference ($P = \cdot 01$) between the 8 varieties in their susceptibility to infestation. Sour orange, sweet orange and orange baladi were highly susceptible while sweet lime and lemon baladi were resistant to infestation.

Effect of Physical and other Environmental Factors. The peak of seasonal abundance of the purple scale was in October when 133·4 scales/leaf were present. The mean monthly temperature during that month in the two years was 20·9° and 23·8°C. respectively, while the mean relative humidity was 80%. The minimum population was found in July when a mean number of 23·7 scales/leaf was counted.

The distribution of the purple scale within the tree was then correlated with height and direction of leaves on two ecologically different groups of trees; sunny group (freely exposed to the sun) and shaded group (surrounded by neighbouring trees in the middle of the orchard).

In winter the distribution of the scales on the two groups was found to depend on the sun. Most of the leaves exposed were more crowded with the scale. The western side of the tree had also more scales. In spring the scales orientated themselves away from the sun. They were found nearer the lower region in the central shaded parts of the sunny trees and in the middle and lower regions of the shaded trees. The lowest population, however, was on the leaves exposed to the sun. In summer, the highest population of the scales was found in the centre of the middle region of the sunny trees rather than on the lower region (where heat reflects back from the ground), or the top region which is well exposed to sun radiation. On shaded trees the insects were found more abundant on the lower and middle regions.

These results may indicate that temperature plays the major role in the distribution of the purple scale on citrus trees under conditions prevailing in Egypt.

NEUERE ERKENNTNISSE ÜBER FLUG UND EIABLAGE DER BRACHFLIEGE (*PHORBIA COARCTATA* FALL.)*

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Die Brachfliege ist ein wichtiger Schädling des Wintergetreides, vereinzelt auch an Sommergetreide. Sie verursacht in manchen Jahren erhebliche Ertragsminderung, bei starkem Befall müssen Getreidebestände sogar umgebrochen werden.

Im Frühjahr 1964 war der Schaden an Winterweizen in der Umgebung von Braunschweig auf schwerem Boden, der nach Zuckerrüben bestellt wurde, sehr beträchtlich. Dabei war bemerkenswert, daß es sich überwiegend um Rübenbestände handelte, deren Reihen im Juli 1963, also zu Beginn der Eiablage, bereits geschlossen waren. Wir fanden also die bestehende Lehrmeinung, daß die Brachfliege zur Eiablage Brachflächen bevorzugt, nicht bestätigt (1, 2, 3, 4).

Das Hauptziel unserer Untersuchungen war zunächst, das Vorkommen der Brachfliege in verschiedenen Kulturen festzustellen und zu prüfen, ob ein direkter Zusammenhang zwischen der Zahl der Weibchen und der Zahl der im Boden gefundenen Eier besteht. Bei positivem Befund könnte an Stelle der Eizahl eventuell die Zahl der Weibchen für eine Prognose-Methode Verwendung finden.

Die Fangmethode der Fliegen und die Methode zur Bestimmung der Eizahl im Boden wurden bereits veröffentlicht (1, 2).

Wir untersuchten drei verschiedenen Befallsgebiete, die folgendermaßen charakterisiert sind:

1. *Rotenburg:* ein Gebiet mit anmoorigem Sandboden; dort traten die Larven stark und allgemein auf (Dauerschadgebiet), Untersuchte Kulturen: Roggen, Hafer, Kartoffeln und Kohlrüben.

2. *Lauenburg,* ein Gebiet mit humusarmem Sandboden, dort trat auch ein starker Befall auf, der aber nicht so weit verbreitet war wie in Rotenburg. Untersuchte Kulturen: wie in Rotenburg, statt Hafer Sommergerste.

3. *Rendsburg,* ein Gebiet mit leichtem Sandboden. Der Befall war dort schwach, Kulturen wie in Rotenburg, Kohlrüben fehlten.

Die Ergebnisse der Untersuchungen können wie folgt zusammengefaßt werden:

(*a*) Die Zahl der Fliegen nahm in der Reihenfolge Rotenburg, Lauenburg und Rendsburg bei allen Kulturen ab, ausgenommen die Kohlrüben in Lauenburg. In den Getreidebeständen wurden weitaus mehr Fliegen gefangen als in den Hackfruchtbeständen.

(*b*) Im Roggen betrug die Fangquote in 60 cm Höhe mehr als die doppelte der in 1·30 m Höhe, also in Ährenhöhe.

(*c*) In Rotenburg wurden im Roggen- und im Haferbestand viele Weibchen gefangen. Im Boden des Roggenfeldes wurden keine Eier gefunden, im Haferfeld nur eine geringe Anzahl (Abb.1) Im dem Kartoffelbestand fanden wir weniger Weibchen, jedoch mehr Eier

* Die Untersuchungen wurden von der Deutschen Forschungsgemeinschaft unterstützt, der auch an dieser Stelle herzlich gedankt sei.

als im Haferbestand. In dem Kohlrübenbestand war die Diskrepanz zwischen Zahl der Weibchen und Zahl der Eier am höchsten.

In Rendsburg waren die Ergebnisse im Roggen ähnlich wie die in Rotenburg. Im Hafer- und im Kartoffelbestand war die Zahl der Weibchen gleich hoch, die der Eier aber im Haferfeld beträchtlich höher als in den Kartoffeln.

Aus diesen Untersuchungen geht hervor, daß eine Relation zwischen der Zahl der Weibchen und der Zahl der im Boden gefundenen Eier nicht vorhanden zu sein scheint und wahrscheinlich keine Prognose-Methode daraus abgeleitet werden kann.

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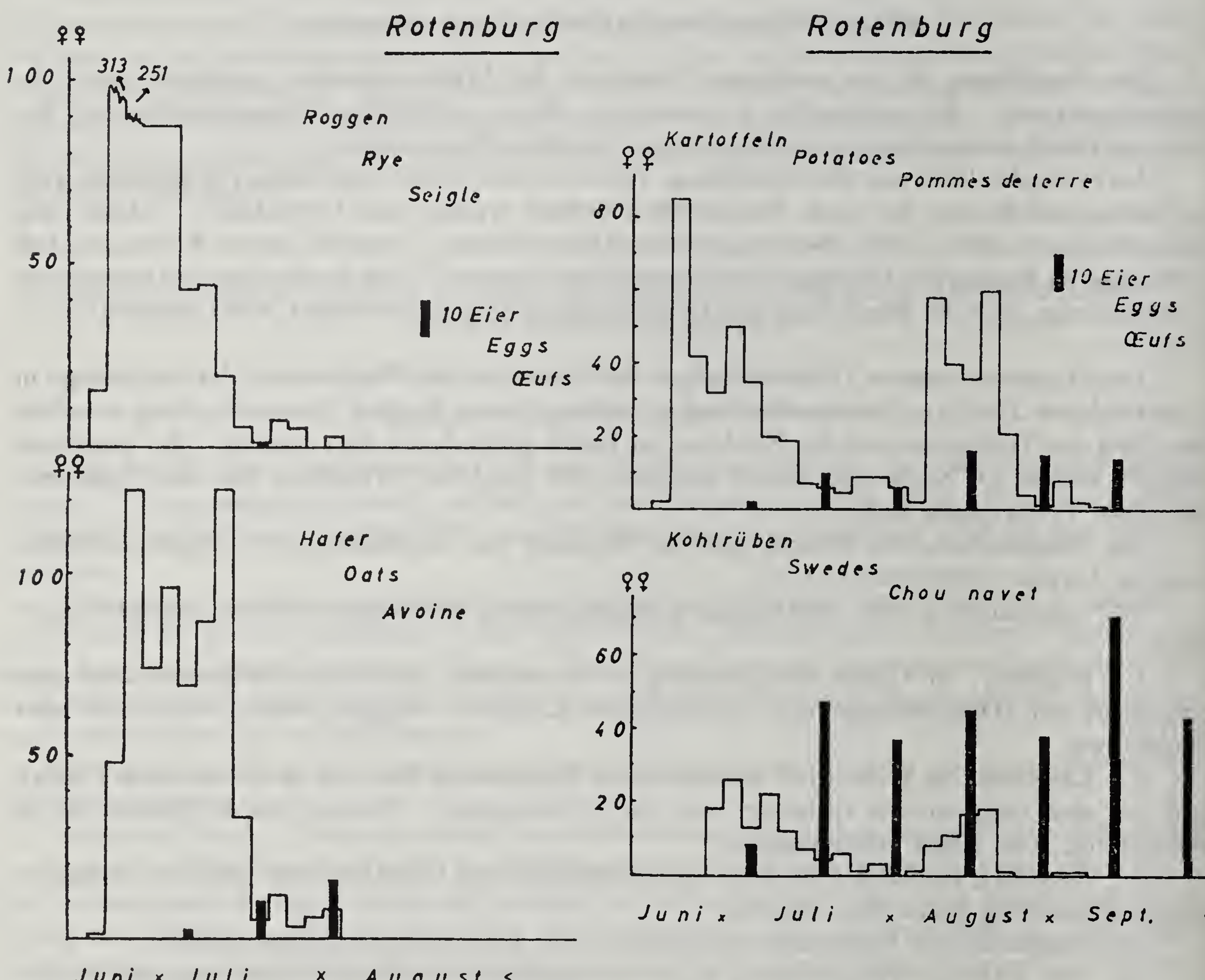

Abb. 1. Zahl der Weibchen an den einzelnen Fangtagen und Zahl der im Boden gefundenen Eier in Roggen-, Hafer-, Kartoffel- und Kohlrüben-bestand in Rotenburg.

BEOBACHTUNGEN ZUM FRASSVERHALTEN DER LARVEN UND IMAGINES VON *APION VIRENS* HRBST. (COL: CURCULIONIDAE)

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Der Curculionide *Apion virens* lebt phytophag an *Trifolium*-Arten, besonders an *T. pratense* und *T. repens.* Während die Larven in den Stengeln minieren, fressen die Imagines längliche oder rundliche Löcher in die Blattspreiten. Das Frassverhalten beider Stadien wurde in Freiland- und Laboratoriumsuntersuchungen ermittelt.

Der Miniergang der Larven verläuft in den ersten Tagen meist direkt unter der Epidermis und kann diese stellenweise durchbrechen. Auch in den späteren Larvenstadien wird der periphere Teil des Stengels bevorzugt. Die Länge des Frassganges nimmt in den ersten Tagen stärker zu als gegen Ende der Entwicklungsperiode. Der Grund liegt in der zunehmenden Durchbohrung von Nodien, welche die Fortführung des Ganges bedeutend hemmen. Besonders bei jungen Larven können diese Knoten zu einer Umkehr der Frassrichtung Anlass geben, vor allem dann, wenn sie stengelaufwärts liegen.

Die Bewegungsrichtung der Larven ändert sich im Laufe der Entwicklung in charakteristischer Weise: während in den ersten Tagen keine Richtung bevorzugt wird, tritt ungefähr vom 6. Tage ab eine Ausrichtung der Larven stengelabwärts ein. Mit zunehmender Verpuppungsbereitschaft ändert sich dann wieder die Richtung, so dass bei etwa 70% der Puppen der Kopf akropetal ausgerichtet ist.

Eine ungewöhnlich hohe Mortalität der geschlüpften Jungkäfer kann bei Frass an der Wiesenform des Rotklees *T. pratense* var. *spontaneum* beobachtet werden: Wegen der kurzen Stengel dringen viele Larven in den Wurzelbereich ein. Findet hier die Verpuppung statt, so kann der geschlüpfte Käfer oft die Wurzel nicht mehr verlassen und geht unausgefärbt zugrunde.

Nach dem Schlüpfen bevorzugen die Imagines in den ersten Tagen die Spitzenhälfte eines Fiederblattes für ihre Frasstätigkeit. Mit zunehmendem Alter wird dann aber der basale Teil bevorzugt. Besonders nach der Überwinterung fressen die Käfer auf diesem Teil 90-100% der Löcher.

Werden Blattober- und -unterseite den Käfern im Versuch unter gleichen Bedingungen geboten, wobei die Unterseite nach oben gekehrt wird, so tritt eine deütliche Bevorzugung der letzteren ein. Entscheidender ist aber noch die Orientierung der Blattfläche: im Wahlversuch wurde in jedem Fall die nach unten liegende Fläche als Ansatzpunkt für den Frass gewählt, gleichgültig, welche Blattseite es war.

Für die unterschiedliche Lage der Frasstellen bei alten und jungen Käfern scheinen morphologische oder physiologische Zustände des Blattes in Verbindung mit einer zunehmenden Erhärtung der Mundwerkzeuge des Käfers verantwortlich zu sein. Das Aufsuchen der basalen Blattunterseite bietet dagegen zweifellos den grössten Schutz gegen Wind, Sonneneinstrahlung, Austrocknung und Feinde.

Das Nagen von Eiablagelöchern beginnt bei den Weibchen bereits im Herbst des Schlüpfjahres, während die Haupteiablage erst im Frühjahr des folgenden Jahres erfolgt. Da aber in Einzelfällen auch schon im Herbst Eier abgelegt wurden, hängt das Nagen von Eiablagelöchern wahrscheinlich mit der Entwicklung der Gonaden zusammen.

Normalerweise treten im Lebensablauf der Imagines 3 Frassperioden auf: Die erste beginnt unmittelbar nach dem Schlüpfen und dauert etwa 3 Wochen. Nach einer Pause von 6 bis 7 Wochen (Ausbreitungsphase) beginnt die 2. Periode, deren Ende durch den Eintritt ungünstiger Temperaturen bestimmt wird. Im nächsten Frühjahr wird etwa ab Mitte März der Frass wieder aufgenommen. Leben die Käfer nach der Fortpflanzungsperiode im Mai-Juni noch, so wird während der Sommermonate der Frass eingestellt und erst wieder im September zusammen mit den Jungkäfern fortgesetzt.

CIRCADIAN RHYTHMS IN THE LEAFCUTTER BEE, *MEGACHILE ROTUNDATA* (FABR.)

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Adult emergence usually occurs from approximately 08·00-12·00 hrs. each day, although some emergence appears in the early afternoon. Mating, on the other hand, although more prevalent in the morning, occurs throughout the day. Since the cells are located in linear series of from 3 to 18 cells in a totally opaque nesting medium, some causal factor other than light was believed to trigger the periodicity. A number of tests indicated that eclosion from the cell (and puparium) proceeds in random fashion throughout the day when held at constant temperatures (26, 29, 32, 35°C). Periodicity was not induced by exposing bare cells to alternating light and dark, but could be readily induced by alternating temperatures of 32:22 and 29:22, with eclosion occurring in the first six hours following return to the higher temperature. A series of experiments revealed that temperature differentials of 3°C was sufficient to fix a diurnal rhythm in populations of this species.

Single exposure to 22° of populations held at constant 32°, in which emergence had already begun, fixed the diurnal emergence rhythm for up to 5 days. A minimum of 2 hours at 22° was sufficient to fix periodicity for 3 days.

Two series of 100 prepupae were held at 32° until 20% of emergence had occurred. One series transferred to 28° and left there until the test was concluded, had no emergence for four days following the temperature change. By the sixth day emergence proceeded in a normal fashion.

Two other series held at constant 32° until 20% emergence. One was moved to 22° for 12 hours, 28° for 6 hours and then to 32° for 6 hours each day. The second was moved to 22° for 12 hours, 32° for 6 hours and to 28° for 6 hours. All emergence occurred only during the first part of the 6 hour period at 32°C. This suggests that the species is conditioned to the highest temperature at which it is kept, and ecloses from the pupa only at that temperature. Modification of this conditioning process requires several days at the new temperature maximum (see below).

There are differential rates of development among the cells in a given series, even when held at constant temperatures throughout the post larval stages. The sides of 50 cell series were cut away so that each prepupa was visible. When pupation of approximately 50% had occurred, all of the series were subjected to 12 hours at 22° and returned to 32° thereafter. Only those that had eclosed as adults but remained in the cell at the time of cold exposure had a fixed emergence periodicity. The remainder (pupae and prepupae) did not show any emergence rhythm. It is suggested that in bees, at least, and possibly in other Holometabola the periodicity can be fixed only in mature adults prior to the time they emerge from the cocoon.

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SECTION 6.—ECOLOGY (INCLUDING CONSERVATION OF NATURE)

The following papers were read but their authors either did not wish them to be published here or the manuscripts arrived too late:

Johnson, C. G. (U.K.). Migratory flight and the reproductive cycle.

Kennedy, J. S., and Way, M. J. (U.K.). Intra-specific mechanisms in insect population regulation.

Messenger, P. S. (U.S.A.). Factors influencing the distribution of three species of parasites of the aphid *Therioaphis* in California.

Montgomery, B. E. (U.S.A.). Influence of photoperiod and temperature upon rate of development of Odonata.

Pradhan, S. (India). A new biotic theory of the periodicity of locust (*Schistocerca gregaria*) cycles.

Townes, M. C. (U.S.A.). Seasonal distribution of Ichneumonidae in Michigan, U.S.A., determined from collections in Malaise traps.

STUDIES OF INSECT POPULATIONS, WITH SPECIAL REFERENCE TO THE ROLE OF HABITAT

BOTTOM FAUNA AND PLANT DETRITUS IN STREAM RIFFLES

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The important ecological problems of determining and accounting for the distribution and abundance of the benthic fauna of running waters are complex and not easily solved. This is partly due to the difficulties of sampling and also to the impracticability of measuring the physical factors operating in streams.

Recent work (1) stressed the importance of disintegrating plant material (plant detritus), mainly of allochthonous origin, in the distribution of many bottom fauna animals in a riffle of a Scottish Highland stream (Shelligan Burn, a tributary of the River Almond, Perthshire). The distributions of the young stages of *Leuctra inermis* Kempny, *Amphinemura sulcicollis* (Steph.) (Plecoptera), *Baetis* spp., *Rhithrogena* spp. (Ephemeroptera) and Chironomidae, together comprising 70% of the bottom fauna collected during a year, were significantly correlated with the distribution of the plant detritus in the riffle.

To investigate the generality of this relationship, samples, containing bottom fauna and plant detritus collected together, were taken by a Surber-type method from riffles of nine Highland streams in February-March, 1964. In each stream there was a close correlation between the distribution of bottom fauna and that of the plant detritus. Most of the variance in the number of animals collected in the samples could be attributed to the amount of plant detritus present, the relationship between the two variates being, in each series of samples, that of the linear regression.

Thus it now becomes possible to estimate the abundance of most of the bottom fauna organisms from a much smaller number of samples than had hitherto been thought necessary, provided the distribution of the plant detritus is adequately described from further samples.

Some preliminary studies on the biological reasons for this distributional relationship between benthic organisms and plant detritus have been carried out. Aggregation of animals on to plant detritus, placed under bricks in trays set into the bed of the stream, was studied. It was shown that a significantly greater number of several abundant species aggregated into the trays that contained the greater amounts of plant detritus. A significantly greater number of individuals of these species aggregated into trays containing plant fragments under bricks, than into trays containing thin rubber fragments placed under bricks, whilst there was no difference between the number of animals aggregating in these latter trays and trays containing bricks only. These experiments suggest that animals aggregate in plant detritus in riffles for food rather than for shelter. The species most closely correlated with the plant detritus all feed on plant detritus.

In seven of the nine streams the percentage composition of the bottom fauna was similar and their faunas can be compared numerically. In the regression equations the rate of change of the number of animals on plant detritus, in general increased with increase in the total concentration of salts and with the concentration of calcium ions in the stream. This may be due to the plant detritus in the chemically richer streams either decomposing at a quicker rate, or being initially more nutritious than the plant detritus in the chemically poorer streams. The classification of the plant detritus and its rate of decomposition is at present being investigated.

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THE EFFECT OF CHEMICAL FERTILISERS ON THE MUD FAUNA OF TWO LOCHS IN THE SCOTTISH HIGHLANDS

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During 1954 and 1955 agricultural fertilisers were added to two lochs situated 1·5 miles (2·4 km) apart in north west Sutherland in an attempt to increase the growth rate of the brown trout *Salmo trutta* L. The physical and chemical characteristics are summarised in Table 1.

TABLE 1

Loch	*Altitude*		*Area*		*Mean depth*		*pH**	*Alkalinity**
	ft	*m*	*acres*	*ha*	*ft*	*m*		*mg* $CaCO_3$/l
Lochan an Smuraich	140	43	5·9	2·4	15	4·6	5·7	1·0
Loch Grosvenor	190	58	6·2	2·5	10	3·1	5·8	2·0

* Before addition of fertiliser

Ground limestone at the rate of 10 cwt/acre (125·5 kg/ha) was added to both lochs to raise the alkalinity and NPK fertiliser and sodium nitrate were added to Lochan an Smuraich and calcium superphosphate to Loch Grosvenor so as to add approximately 25-30 lb phosphorus per acre (28-33·5 kg/ha). The alkalinity rose to a maximum of 5·0 mg $CaCo_3$/l at Smuraich and 7·2 mg $CaCO_3$/l at Grosvenor within a week of the addition of limestone, after which the levels declined to those prior to the addition by 1956.

Quantitative samples of the invertebrate fauna of the mud at a depth of 5 m were taken with an Ekman grab in April and October from 1954 to 1961 with the exception of October, 1955, 1960 and 1961. The mud fauna was very sparse prior to fertilisation (total biomass, fresh weight 0·8 and 0·4 g/m^2 at Smuraich and Grosvenor respectively) and consisted chiefly of Chironomidae larvae with a few other insects, Oligochaeta, Sphaeriidae and Hydracarina.

There was no change in the total weight of bottom fauna in 1954 and 1955 but at both lochs an increase occurred in 1956 reaching a maximum in April 1957 when sixteen times the prefertilisation biomass was recorded at Lochan an Smuraich and twenty-five times at Loch Grosvenor. The total weight fell to about one half to a third of this level in April 1958 and 1959 and returned to the prefertilisation level in 1960 and 1961. Thus the maximum production occurred two years after the last application of fertiliser and the biomass returned to the original trophic level five years after. At both lochs the increased biomass was brought about chiefly by a rise in the number of Chironomidae, the other groups showing slight or no response. The total numbers of organisms also reached a maximum in April 1957 at Lochan an Smuraich at 9 times the number in April 1954. They remained high in the spring of 1958 and 1959, in spite of the decline in total biomass, and were much lower in 1960 and 1961 although still two to three times the prefertilisation level. At Loch Grosvenor high numbers were recorded from October 1956 although the maximum was not reached until April 1959 at 43 times the catch in April 1954. After this the total numbers declined rapidly and were of the same order as prior to fertilisation in April 1961. Initially, at both lochs, the larger species of chironomid increased rapidly and were the cause of the maximum in total biomass in April 1957, after which there was a change in the composition of the chironomid fauna, smaller species increasing and being very abundant three to five years after the last fertilisation. The species of Chironomidae had not completely reverted to pre-fertilisation proportions when the last samples were taken in April 1961.

Measurements of the growth rate of trout up to 1957 are recorded by Munro (1) from which it appears that the trout did not utilise the increased production of chironomid fauna efficiently. This may have been because the larvae and pupae were only available to trout for a limited period of the year and that the winter feeding in particular was little better than prior to fertilisation. In future experiments it might be profitable to introduce suitable food organisms such as *Gammarus* spp., *Asellus* spp., and *Limnaea peregra* Müll. following the initial application of fertiliser.

The increases in mud fauna showed that the calcium superphosphate produced at least

as good an increase in the insect biomass as the more expensive NPK fertiliser. If the biomass is to be maintained at a high productive level fertiliser would have to be added at least every second year.

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OBSERVATIONS SUR DES POPULATIONS DE *SIMULIUM DAMNOSUM* THEOBALD, 1903 (DIPTERA, SIMULIIDAE) EN ZONE DE GITES NON PERMANENTS

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En Afrique tropicale d'importantes populations de *S. damnosum*, vecteur de l'Onchocercose humaine, existent dans des régions où les rivières ne sont pas permanentes. La survie de l'espèce pendant la saison où n'existent pas de gîtes en activité ne semble pouvoir actuellement être attribué ni aux oeufs ni aux larves ni aux nymphes. En ce qui concerne les femelles deux hypothèses ont été formulées: selon l'une elles seraient capables de survivre, en vie ralentie, sur place dans des abris; selon l'autre elles réenvahiraient les zones sèches chaque année à partir de foyers permanents.

Trois ans d'observations ont été effectuées en Haute Volta sur des populations de *S. damnosum* en zone sèche. Ces observations comprenaient: étude des gîtes préimaginaux, captures de femelles sur appât humain de 06 heures à 18,30 h., dissection de ces captures pour étude de l'âge physiologique.

L'analyse des résultats a mis en relief un certain nombre de faits. Dans les zones de gîtes non permanents les femelles de *S. damnosum* cessent de venir piquer l'homme dès que les cours d'eau ne coulent plus, peu après la disparition des stades préimaginaux. Les derniers stades présents dans ces gîtes sont des larves de 7è stade et des nymphes. Au cours des dernières semaines d'activité des femelles la proportion de nullipares augmente jusqu'à etre supérieure à celle des pares. Ce dernier phénomène n'a pu etre relié aux conditions écologiques; en effet dans l'est de la Haute Volta il survient en saison fraiche (basses températures de l'air et de l'eau, hygrométrie très basse) et dans l'ouest en saison chaude (hautes températures de l'air et de l'eau, hygrométrie moyenne).

Les modalités du retour à l'activité des femelles varient selon les localités et les années et semblent coincider avec les facteurs suivants: durées de l'interruption du cours des rivières, distance des gîtes permanents.

Pour une même zone de gîtes lorque la période d'interruption est longue les premières captures qui la suivant sont formées de femelles dont l'âge physiologique est beaucoup plus élevé que lors des dernières captures précédant cette interruption. En cas de saison sèche courte les populations récoltées avant et après sont d'âge physiologique voisin.

Dans les parties aval des rivières, les plus proches des gîtes permanents, des femelles isolées ou en petit nombre viennent piquer dans les semaines précédant la saison des pluies. Dans les zones plus éloignées la rapparition se produit de plus en plus tard, soit dès les premières pluies, soit après un certain délai.

Cet ensemble de faits nous parait être en faveur plutôt d'une réinvasion à partir de foyers permanents que d'une survie sur place. On peut peut-être voir une confirmation de cette hypothèse dans la rencontre de stades saucisse d'Onchocerca chez une femelle, en début de pluies, cent jours après les dernières captures de la saison précédente.

BUTTERFLIES OF CHALK GRASSLAND: A CONSERVATION PROBLEM

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The chalklands of Britain lie in South and East England, extending as far North as Yorkshire, and West to the borders of Devon. Following the last glaciation, the recession of the ice (which had extended almost as far South as the Thames) was succeeded by the natural growth of forest on the chalk. Early man cleared areas of this for cultivation, and these were then allowed to revert to grassland which has since had a long tradition of grazing, usually by sheep. Over the centuries a very interesting flora and associated fauna has built up: often, the places of greatest scientific interest are associated with the field systems or earthworks of prehistoric man. The gradual development of the typical habitat may be exemplified by the finding (1) that the grass *Zerna erecta* has not reappeared 70 years after the last cultivation, even where pure stands of it are immediately adjacent.

Much chalk grassland remained under traditional grazing management until the last 25 years. Since the War, this has declined sharply: a major factor has been the dying out of the oldtime shepherd who "drifted" the sheep across the Downs by day and brought them back to the farm by night. Sheep now have to be fenced on the land, and water has had to be laid on. In addition, the growing of barley on the chalk has become very profitable, and the recent development of new machinery and agricultural methods has enabled the cultivation of remarkably steep slopes.

Now only relatively small pockets of typical old chalk grassland remain. Further, the almost complete disappearance of the rabbit following the introduction of myxomatosis in 1953 has resulted in a massive upgrowth of scrub and coarse herbage in these little-grazed areas. Places where adequate grazing of chalk grassland continues so that they show a short sward with associated yews and beechwood are very few.

Typical butterflies of chalk grassland are *Lysandra coridon* Poda, *L. bellargus* Rott., *Hesperia comma* L. and *Melitaea aurinia* Rott., though the last is also found in damp habitats. Where the vegetation has grown up, there has been a very marked drop in their numbers. Both sites studied have shown this in the two *Lysandra* species (2) while in one of them *L. bellargus* has become extinct within three years of a period of plenty. *H. comma* has vanished completely from both sites; and even the ubiquitous *Maniola jurtina* L., which requires long grass, has diminished markedly in numbers. Probably the sequence of events is invasion of scrub and coarse herbage, colonisation of this by voles (*Microtus agrestis* L.), use of vole runs by shrews (*Sorex araneus* L.) which prove to be major predators of the early stages, especially the pupae.

Another serious point is that, even where the food plants colonise new areas, the present isolated insect colonies cannot easily spread to these, as they could when long continuous tracts of downland existed.

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TORTRICID FAUNA (LEPIDOPTERA: TORTRICIDAE) OF NATURALISED *MALUS PUMILA* MILL. TREES: A PRELIMINARY REPORT

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The domestic apple, *Malus pumila* Mill., which was introduced to North America from Europe during colonial times now commonly occurs as an escape in New York. Ecologically, the naturalised plant is classed as a woody pioneer or sub-climax species. Stands of *M. pumila* ranging up to 100 acres or more in extent, are often found in pasturelands where they have been "planted" through the fecal droppings of the dairy cow. Apple may occur here either in a near-pure state or share the site with native species of *Crataegus*.

Many American arthropods have adopted *M. pumila* as a host. In undertaking a study

of the nature and extent of this acceptance, the writers have elected to limit intensive faunal observations to the lepidopterous family *Tortricidae* as defined by Obraztsov (Tijdschr. v. Ent. 97: 141-231, 1954; *Ibid*, 98: 147-228, 1955). He gives the olethreutids, tortricids and sparganothids sub-family status. *Crataegus* was selected to represent the native flora in host specificity and host origin considerations.

Thus far, 42 tortricids have been found feeding on apple in New York. The sub-family *Olethreutinae* is represented by 14 species, the *Tortricinae* by 24 species and the *Sparganothinae* by 4 species. Five species are exotics, namely, *Grapholitha molesta* Busck, *Hedia nubiferana* Haw., *Spilonota ocellana* D. & S., *Carpocapsa pomonella* L. and *Archips rosana* L. At least 20 of the 42 species feed to a greater or lesser extent on apple fruits. A provisional key has been prepared for the field identification of the larvae.

Most of the tortricids found on apple also use *Crataegus* as a host. While this situation indicates a fairly close host kinship, it also could mean that most of the *M. pumila* tortricids are rather polyphagous feeders. However this may be, in quantitative sampling studies involving known (*Archips argyrospila* Wlk. and *Choristoneura rosaceana* Harr.) and suspected polyphagous feeders, the two host groups proved equally attractive. Evidence based on the more specialised and restrictive feeders is more divergent. Thus, the leaf-folding species *Anchylopera nubeculana* Clem. in the presence of apple, *Amelanchier* and *Crataegus* shows a definite preference for the first two hosts. Failure of *Carpocapsa pomonella* L. to accept the fruit of *Crataegus*, generally, probably means that the fruits of most species are too small to accommodate this large internal fruit feeder. Supporting this assumption is the fact that it accepts such diverse larger fruits as apple, plum, apricot and English walnut, *Juglans regia* L. Probably the most distinctive example of selectivity among tortricids is found among three species of *Eucosmini*. Between apple and *Crataegus*, *Pseudexentera mali* Free. feeds almost exclusively on apple. (Its original host may have been the native crabapple *Malus coronaria* Mill.) The other two, *Pseudexentera maracana* Kft. and *Epinotia* sp. have never been found on apple being strictly *Crataegus* feeders.

The American tortricids and other arthropods that have adopted *M. pumila* as a host include many species that had *Cratageus* as an original host. However, the writers believe the arthropod host kinship between apple and *Crataegus* is not particularly close.

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POPULATION GROWTH IN FOOD RENEWAL EXPERIMENTS WITH INSECTS

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Smith (1954) considered that the growth of a population which experienced a regular food renewal would first show sigmoid growth and then oscillate with a periodicity determined by the renewal frequency. He postulated that to avoid these oscillations, a continuous food supply should be available; a population would then show sigmoid growth with a clearly defined smooth upper asymptote. Smith (1963) approximated to continuous by daily feeding hoping thereby to achieve this population growth pattern.

Would any real species growing in restricted conditions be likely to achieve this ideal growth pattern? Consider the case of an insect species with two passive stages (eggs and pupae), one active feeding stage which when of high density is likely to suffer solely from food shortage, and a short lived, non-feeding adult stage unlikely to suffer from density effects (*Lasioderma serricorne* (F.) is such a species; Lefkovitch and Currie, 1963). The effects of food shortage are predictable, namely, high larval mortality, prolonged larval development, the surviving larvae giving rise to adults of low weight and fecundity. Initially the growth of a population of such a species experiencing a regular food renewal would be Malthusian (taking into account the changing population structure) and would later tend towards the Malthusian stable state with a periodicity determined by the length of a generation. The amplitude of this oscillation would diminish the longer the process continues. When the food removed by the

exponential growth of the population had exceeded the arithmetical addition of food, the population might have any structure. Whereas the eggs, pupae and adults would continue to perform normally, the larvae would show prolonged development and reduced survival. Consequently, the population would tend to be composed primarily of larvae and eventually its size would fall. Since any adults formed would be small and have low fecundity, food would tend to accumulate. The cycle would then repeat itself.

Similar cycles can originate from some other group effects or from some combination of them, e.g. see Frank (1957); however, Cole's contention (Cole, 1951) that such cycles are essentially the result of random occurrences must be unsound. This is not to say that there are no important chance happenings or that cycles due to other causes may not also occur.

There is a very close physical analogy to this system. An object showing simple harmonic motion ($\equiv$ the length of a generation) which is damped ($\equiv$ the overlap of the generations) and subject to a periodic external force ($\equiv$ e.g. the food renewal) would oscillate in a very similar manner. The equations for this motion are well known and are given in virtually every text on applied mathematics.

Since most species grow in limited conditions, I believe that the so-called stationary state of a population of any species is a theoretical fiction.

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STUDIES OF INSECT POPULATIONS, WITH SPECIAL REFERENCE TO THE ROLE OF NATURAL ENEMIES AND CLIMATE

THE ROLE OF COLEOPTERA IN THE NATURAL CONTROL OF MOSQUITOES IN CANADA

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To develop an integrated biological and chemical control program (3, 16, 17, 22), the habits and ecology of the predators of mosquitoes need to be studied in greater detail and such a study is in progress in Canada.

Hinman (11) listed 24 species of Coleoptera as mosquito predators. Many of these records are open to question, however, as the predators were confined to laboratory aquaria where conditions make it difficult to relate the results to pool conditions. Some of the limitations of this method were avoided in the determination by means of a radioactive tracer

technique (2, 14) that 9 species of Dytiscidae, 1 gyrinid, and 1 hydrophilid were predators in natural pools near Belleville, Ontario. A similar study of the rockpool mosquito, *Aedes atropalpus* (Coq.) and three associated culicids (15) demonstrated that 6 species of Dytiscidae were predators.

Stage and Yates (21) reported aedine eggs destroyed by Carabidae. This was confirmed in recent field experiments near Belleville, Ontario, in which adults of *Agonum* sp., *Bembidion frontale* (Lec.), *B. muscicola* (Hayw.), and *Pterostichus leconteianus* Lutsh. fed on eggs of *Aedes* spp. that had been tagged with radioactive phosphorus, P^{32}.

Dissection and examination of the digestive tract showed a total of six species of field-collected Dytiscidae, Gyrinidae, and Hydrophilidae to be predators (14). The precipitin test (7) also identified water beetles as predators and indicated that large rather than small beetles fed on *Aedes*. Other Coleoptera were reported from field observations (6, 8, 9, 12, 18, 20).

The biology of Nearctic predacious water beetles as summarized by Balduff (1) refers mainly to species in fishponds and other permanent waters. In Ontario, predators in semi-permanent pools have one generation a year, hibernate as adults, and are present during mosquito development. Some species are more active than others at low temperatures and can feed on early-stage *Aedes* which are numerically dominant organisms in early April. *Agabus erichsoni* G. & H. deposits eggs at pool margins during May and these hatch with the mosquito eggs in the following March or April. The three larval stages are well synchronized with *Aedes* larval development. Other species follow later.

Some studies have shown that, in general, the aggregate predation by aquatic beetles can be sufficient for effective control (16) and can curtail the reproduction of other mosquitoes for several weeks after the univoltine species have left (14, 19). As shown also for other predators (5), the degree of control may not be apparent until the predators are removed.

Data from area sampling near Belleville (2, 14) showed that an average population of 4·8 water beetles per square metre contributed largely to a reduction per cent of the *Aedes* larval population by 40·0. In some cases larval populations appeared to be mainly regulated by a single species. This was attributed to the feeding habits of the prey (13, 15).

Existing information indicates, therefore, that aquatic Coleoptera can be quite effective agents of mosquito control. Future lines of research should include detailed studies of the habits, life-history, and effectiveness of the predators and of their tolerance to insecticides. The possibility of introducing more efficient predators of mosquito eggs and of water beetles more tolerant of low temperatures during mosquito larval development needs also to be explored.

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THE ECONOMIC SIGNIFICANCE OF PARASITIC CYNIPOIDEA ASSOCIATED WITH APPLE IN THE NETHERLANDS

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A number of parasitic Cynipoidea associated with apple aphids have been bred in the Netherlands.

Three species of Cynipidae Charipinae were bred as hyperparasites from aphids that had been parasitized by primary Aphidiid parasites (Hymenoptera). *Alloxysta* sp. was bred from the apple-grass aphid, *Rhopalosiphum insertum* Wlk., through the primary parasite *Monoctonus cerasi* Hal. *Charips* sp. was bred from the rosy apple aphid, *Dysaphis plantaginea* (Pass.), through the primary parasite *Ephedrus persicae* Froggatt (= E. *nitidus* Gahan = E. *pulchellus* Stelfox). In some cases this hyperparasite was also bred from the apple-grass aphid through *Monoctonus cerasi*. *Alloxysta gautieri* Kieff. was bred from the green apple aphid, *Aphis pomi* Geer, through the primary parasite *Binodoxys angelicae* (Hal.).

A number of species of Figitidae Anacharitinae have been bred from cocoons of Hemerobiidae (Neuroptera) collected from trapping bands around the stems of apple trees. The parasites were possibly *Anacharis typica* Wlk., *A. ensifera* Wlk., *A. immunis* Wlk. and *Xyalaspis subulifera* Thoms.; the Hemerobiid adults bred were *Boriomyia betulina* Strøm, *B. subnebulosa* (Steph.) and *Hemerobius humulinus* L. It may be possible that these Hemerobiidae had not been preying on apple aphids, but on aphids on weeds in the orchard. However, what is thought to be *Anacharis immunis* was also bred a few times from cocoons of *Hemerobius humulinus*, preying as a larva on the green apple aphid. *Melanips* sp. (Figitidae, Figitinae) was bred from puparia of Diptera that were preying in the larval stage on the rosy apple aphid and the green apple aphid. The hosts were *Leucopis puncticornis* Meig. complex (probably *albipuncta* Zett. = ? *melanopus* Tanasijtschuk) and *L. aphidivora* Rondani (Chamaemyiidae).

Finally, *Callaspidia dufouri* Giraud (Figitidae, Aspiceratinae) was once bred from a puparium of *Lasiopticus seleniticus* (Meig.) (Diptera, Syrphidae), found as larva, preying on the rosy apple aphid.

As all hosts of the above-mentioned Cynipoid parasites, associated with apple, are beneficial parasites or predators of apple aphids, the whole group of the Cynipoidea must be considered as harmful to fruit-growing. Considering the host ranges of the different sub-families of the Figitidae and Cynipidae, only one minor pest of apple might be expected to have a Cynipoid parasite, viz. *Phytomyza heringiana* Hendel (Diptera, Phytomyzidae), the larva of which mines in apple leaves. Some species of Cynipidae Eucoilinae, that parasitize Phytomyzidae, are known from the literature, but none is known to parasitize *Phytomyza heringiana*, nor have we ever bred such a parasite ourselves. It is evident that, as in other Hymenopterous parasites, many groups of the Cynipoidea are in urgent need of taxonomic revision. This is of great importance to practical entomologists, engaged in synecological studies.

Thanks are due to Prof. Dr. M. Principi, Bologna, Italy, who identified the Hemerobiidae, to Dr. M. Mackauer, Belleville, Canada, who identified the Aphidiidae, to Dr. G. Morge, Eberswalde, near Berlin, Germany, who identified the Chamaemyiidae, and to Mr. J. Quinlan, London, England, who identified most of the Cynipoidea.

ZUR NATÜRLICHEN REGELUNG DER MASSENVERMEHRUNG VON *THECODIPLOSIS BRACHYNTERA* SCHWAEGR.: (DIPTERA: CECIDOMYIIDAE) DURCH DEN PARASITEN *MISOCYCLOPS PINI* KIEFF. (PROCTOTRUPOIDEA: SCELIONIDAE)

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Die Untersuchungen an der Kiefernnadelgallmücke *Thecodiplosis brachyntera* Schwaegr. in den Jahren 1959 bis 1963 bestätigten in den Schadgebieten der Staatlichen Forstwirtschaftsbetriebe Neuruppin, Kyritz und Roßlau, daß der weitgehend spezialisierte Endoparasit

Misocyclops pini Kieff. in der Lage ist, Massenvermehrungen der Kiefernnadelgallmücke zu Ende zu bringen. Durch die in regelmäßigen Abständen durchgeführten Untersuchungen an den Gallmückenlarven auf Parasitenstadien konnten etwa mit den Angaben von Stellwaag (1921) zu vergleichende "Cyclopoidlarven" von Mitte Juli an gefunden werden. Die Junglarven waren vorwiegend paarweise, in einzelnen Fällen auch in Tetraden zumeist am Gewebe im Vorderteil der Wirtslarven oder auch zwischen den Malpighischen Gefäßen verankert. Apode Parasitenstadien wurden ab Anfang August im Innern der Wirtslarven ermittelt. Ein Anstieg des Anteils an Junglarven von *Misocyclops pini* Ende September ist sehr wahrscheinlich auf eine erneute Parasitierung durch die im August/September geschlüpften Imagines dieses Endoparasiten zurückzuführen. Die Ermittlungen über den Gesundheitszustand des Schädlings- und Parasitenmaterials und Haltung desselben unter Freiland-, Laboratoriums- und Kühlschrankbedingungen ergaben, daß die nützlichen Schlupfwespen zur Uberwinterung am besten in Gazebeuteln unter Freilandbedingungen gehalten werden können.

Dadurch ist es möglich, rechtzeitig eine Einschätzung über den Parasitierungsgrad der Schädlingspopulation geben und Entscheidungen über die Notwendigkeit von Bekämpfungsmaßnahmen einschließlich der interarealen Übersiedlung der Schlupfwespen *Misocyclops pini* treffen zu können. In einem Einsatzversuch wurden im Frühjahr 1962 zu 70-80% parasitierte Schädlingsstadien aus dem Gebiet von Kyritz etwa 14 Tage vor Beginn des Mücken- und Parasitenfluges nach dem Forstwirtschaftsbetrieb Roßlau überführt (Parasitierung 20%). Durch den im Gebiet von Roßlau schon vorhandenen hohen natürlichen Parasitierungswert ist das Versuchsergebnis nicht überzeugend genug ausgefallen. Es konnte dort, wo die Parasitierungsstadien angereichert worden waren, ein höherer Parasitierungsgrad von etwa 10% festgestellt werden. Beim Vergleich der Parasitierung der Schädlingspopulation in den Jahren 1962 (10-18%) und 1963 (50—80%) ergab sich eine signifikante Differenz (4 600 untersuchte Schädlingslarven).

Zur interarealen Übersiedlung der Parasitenstadien werden die befallenen Kiefernnadeln erst in den Monaten März/April abgestreift und übertragen. Die Nadeln werden in größere, lichtdicht verkleidete Glasstutzen gebracht, die mit Fließpapier ausgelegt und mit Perlongaze (Maschenweite 0,45 × 0,45 mm) überspannt sind. Die schnellbeweglichen Scelioniden können durch die Perlongaze hindurchgelangen, während die größeren Gallmückenimagines im Glasgefäß verbleiben und dadurch ausgeschaltet werden. Die Glasstutzen müssen regensicher auf der Kiefernkultur aufgestellt werden. Der Endoparasit *Misocyclops pini* erwies sich sowohl in Freilandpopulationen als auch nach Anreicherung auf Kiefernkulturen als ein wirksamer Faktor zur Begrenzung der Massenvermehrung von *Thecodiplosis brachyntera*.

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BEITRAG ZUR KENNTNIS EINIGER TACHINEN VON KIEFERN-SCHADLEPIDOPTEREN

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Phryxe erythrostoma Htg. ist nach Herting (1960) die spezifische Tachine des Kiefernschwärmers (*Hyloicus pinastri* L.); sie kann sich nach unseren langjährigen Zuchten aus dem Probesuchmaterial der Kiefernforstämter Nordbadens, der Pfalz und des Saarlandes bis zu 21

Exemplaren in einem Wirt entwickeln. In der Regel verlassen ihre Larven die Schwärmerpuppe im Frühjahr nach der Wirtsverpuppung.

Nachfolgend werden Ausnahmen berichtet, die wahrscheinlich im Freiland und auch bei anderen Wirt-Parasit-Verhältnissen häufiger vorkommen.

Von einer Kiefern-Samenplantage aus dem Kaiserstuhl/Baden wurden am 27.9.1963 drei äußerlich gesunde, ausgewachsene Raupen des Kiefernschwärmers zur Weiterzucht in unser Institut gebracht. Nach drei Fraßtagen ging eine Raupe zur Verpuppung in den Zwingerboden. Die beiden anderen Tiere blieben auf der Oberfläche, ihre Bewegungen wurden nach anfänglicher großer Unruhe langsamer und sie schrumpften, noch lebend, zusammen. Am 6.10.1963 bohrten sich zwei bzw. sechs Tachinenmaden an zwei bzw. vier Stellen durch die Raupenhaut und verpuppten sich in unmittelbarer Nachbarschaft der Raupenmumien dicht unter der Bodenoberfläche. Die erste Fliege schlüpfte am 17.10.1963, zwei weitere folgten erst am 2.11.1963, während die restlichen fünf Tönnchen eingingen. Die geschlüpften Tiere waren normale ♀♀ von *Phryxe erythrostoma* Htg. Für Bestimmung bzw. Bestätigung der ausgezüchteten Tachinenarten bin ich den Herren Dr. Herting und Dr. Kirchberg dankbar. Schon Ratzeburg (1844) berichtet, daß *Musca* (*Tachina*) *erythrostoma* Htg. bereits aus der Wirtsraupe schlüpfen kann. Diese Ausnahme wurde meines Wissens bislang nicht im Schrifttum bestätigt.

An Probesuchmaterial mehrerer nordbadischer Reviere des Winters 1958/59 konnte die schon von Hartig (1840) berichtete Möglichkeit des Überliegens von Kiefernschwärmerpuppen bestätigt werden: Zehn der im Sommer nicht geschlüpften, gesund erscheinenden und weiter isoliert gehaltenen Puppen ergaben zwischen 20.6. und 4.7.1960 sechs normale Falter (2 ♂♂, 4 ♀♀); zwei Puppen lieferten am 10. und 14.6.1960 je zwei Tachinenmaden, aus denen am 25., 27. und 30.6. und 5.7.1960 je zwei ♂♂ und ♀♀ von *Phryxe erythrostoma* Htg. schlüpften. Die beiden restlichen Schwärmer-Puppen gingen ein. Damit konnte auch das Überliegen der Tachinenlarven nachgewiessen werden.

Aus Suchmaterial des Winters 1955/56 von Philippsburg, Nordbaden, schlüpfte normal und anscheinend gesund am 28.5.1956 ein ♀ des Kiefernschwärmers, das mit Essigsäureaethylester abgetötet und dann gespannt wurde. Am 6.6.1956 bohrten sich aus der rechtsseitigen Intersegmentalhaut des toten Falters zwischen 2./3. Tergit und 2./3. Sternit drei Tachinenmaden heraus, die sich in der Spannbrettfuge zu Tönnchen umbildeten. Daraus schlüpfte am 10.7.1956 je ein ♂ und ♀ von *Phryxe erythrostoma* Htg., während das dritte Tönnchen nicht zur Entwicklung kam. Ein derartiger Vorgang ist mir noch nicht bekannt geworden.

In den Jahren 1956 bis 1964 erhielten wir aus Material von Probesuchen die Kiefernspanner-Tachine *Eucarcelia rutilla* Vill. in 68 Exemplaren (33 ♂♂ und 35 ♀♀), von denen 67 Tiere aus *Bupalus piniarius* L. und eins aus *Semiothisa liturata* Cl. gezogen wurden. In der Literatur (1956, 1960) wird die Auffassung vertreten, daß *Eucarcelia rutilla* Vill. wie die den gleichen Wirt parasitierende *Blondelia piniariae* Htg. ihre Wirtspuppe bereits als Larve durch die abdominalen Intersegmentalhäute verläßt, um sich im Boden zu verpuppen. Wir konnten demgegenüber feststellen, daß sämtliche unserer *E. rutilla*-Imagines direkt aus der Wirtspuppe, in sechs Fällen sogar aus in der Puppe bereits voll ausgebildeten Faltern schlüpften. Außer einem Tönnchen, das mit dem Kopfteil zum Wirtsabdomen zeigte und dessen Imago dort die erste Intersegmentalhaut durchbrechen mußte, lagen alle Tönnchen mit dem Kopfende im Kopf der Wirtspuppe, deren Flügel-, Antennen- und Beinscheiden sowie Vorderteile des Puppenkopfes oben und seitlich an den üblichen Reißstellen losgelöst und in einem Stück leicht abgehoben waren.

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MASSENVERMEHRUNGEN FORSTSCHÄDLICHER INSEKTEN ÖSTERREICHS IN IHRER ABHÄNGIGKEIT VON UMWELTFAKTOREN

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Die Verteilung der als mehr primär geltenden forstschädlichen Arten unter den Lepidopteren, Tenthrediniden, Coleopteren und Homopteren gibt Hinweise darauf, daß die in den einzelnen Wuchsgebieten durch klimatische Einflüsse bedingten und begünstigten phytophagen Insekten unserer Holzarten vor allem da als gefährliche Massenschädlinge anzutreffen sind, wo die die Wälder bildenden Holzarten in ihrem Aufbau und in ihrer Zusammensetzung von den naturgegebenen Verhältnissen weit abweichen oder wirtschaftliche Maßnahmen in ihrer Struktur sie ungünstig beeinflussen. So treten im pannonischen und pannonisch beeinflußten Klimagebiet Österreichs mit den naturgegebenen Eichen-Hainbuchenwaldungen in den künstlichen Kiefernaufforstungen sehr viele Großschädlinge der Kiefer auf, wie *Bupalus piniarius* L., *Dendrolimus pini* L., *Rhyacionia buoliana* Schiff., wobei in den sogenannten Wassermangelgebieten Gradationen im größten Ausmaße sich abspielen. In den den Alpen vorgelagerten Gebieten im Norden und Osten Österreichs und in den Beckenlandschaften Kärntens ist *Pristiphora abietina* Christ. überall da zu finden, wo die Fichte nicht standortsgemäß ist oder einen zu großen Prozentsatz in den Mischwaldungen einnimmt. *Dreyfusia nusslini* C.B. hat sich in den Tannengebieten Österreichs da besonders ausgebreitet, wo Jungtannen unter zu starkem Lichteinfluß stehen oder unter Wildschäden leiden. *Zeiraphera diniana* Gn., ein Massenschädling der Lärche besonders im Hochgebirge, befällt die Lärche vor allem da, wo sie in Reinbeständen stockt. Lärchenreinbestände entwickelten sich vielfach auf Rodeflächen, wie sie zur Weide- und Mahdgewinnung im Hochgebirge angelegt wurden.

Diese Ausführungen weisen darauf hin, daß zweifellos der Zustand der Wirtsbäume dafür ausschlaggebend ist, ob bestimmte Waldgebiete zu Stätten gefährlicher Massenvermehrungen von Forstschädlingen werden können.

Dies zeigt sich auch noch bei Kalamitäten von Laubholzschädlingen in den natürlichen Eichen-Hainbuchenwaldungen Österreichs, wo die stärksten Schäden besonders an freistehenden Eichen, sogenannten Wertholzeichen, zu finden sind.

Schädlingsmassenvermehrungen sind aber auch in wirtschaftlich nicht oder sehr wenig beeinflußten Waldgebieten zustande gekommen; so hat sich vor allem auch im Urwald Rothwald im Dürrnsteingebiet eine Massenvermehrung von *Hibernia defoliaria* L. im Jahre 1958 abgespielt; weiters waren bemerkenswert Massenvermehrungen von *Himera pennaria* L. in natürlichen Laubwaldungen des Leithagebirges und von *Diprion pini* L. an natürlichen Fichten-Kiefer-Lärchenstandorten im Oberinntal Tirol. Diese Massenvermehrungen sind aber schon nach einer Generation durch Einwirkung biotischer Umweltfaktoren (Parasiten, Krankheitserreger) zusammengebrochen.

Bemerkenswert ist auch, daß bei Kalamitäten von forstschädlichen Insekten im Osten Österreichs, wo die klimatischen Verhältnisse für Arthropoden—sofern sie harte Winter ertragen können—optimal sind, häufiger auch ein zahlenmäßiges Ansteigen dieser Arten oft bis zum Ausmaß kleinerer, örtlich begrenzter Massenvermehrungen auch im Westen Österreichs besonders in föhnbeeinflußten Lagen zu beobachten ist, so bei den letzten Massenvermehrungen des Kiefernspanners, *Bupalus piniarius* L. und des Kiefernspinners, *Dendrolimus pini* L. Dies weist darauf hin, daß auch großräumige Faktoren für die Auslösung von Massenvermehrungen eine entscheidende Rolle spielen dürften. Ob günstige Temperatur-Feuchtigkeitskombinationen zur Klärung des plötzlichen Ansteigens der Vermehrungsenergie (jedenfalls begünstigen sie das Durchkommen der Junglarven der nächsten Generation-) allein genügen ist eine weitere Frage, die noch eingehenderer Untersuchungen bedarf. Nach Vergleich—der Aufzeichnungen der Schädlingskalamitäten Osterreichs der letzten 80 Jahre (1) mit Aufzeichnungen der Sonnenaktivität des gleichen Zeitraumes—durch H. Gheri scheinen sich Hinweise auf Zusammenhänge von Insektenmassenvermehrungen mit der allgemeinen Sonnenaktivität in der Weise zu ergeben, daß der Ausbruch von Kalamitäten zur zeit intensiver Sonnentätigkeit unwahrscheinlicher wird und häufiger auszubleiben scheint.

Zweifellos vom Zustand und Ausmaß der vorhandenen Nahrung abhängig ist—soferne die

klimatischen Bedingungen optimal sind—das Zustandekommen von Massenvermehrungen von holzzerstörenden Insekten, die besonders auch in nicht standortsgemäßen Nadelholzbeständen in Massen auftreten. Unter entsprechenden kleinklimatischen Einflüssen, insbesondere jenen der Strahlung, können jedoch auch im Hochgebirge bei entsprechendem Anfall von Schadholz Kalamitäten dieser Arten entstehen.

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THE PINK BOLLWORM (*PECTINOPHORA GOSSYPIELLA*) IN YUGOSLAVIA

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The pink bollworm was first reported at Bar (Montenegro) in 1951 (2) having almost certainly arrived from Albania. Despite steps to exterminate it, it was again discovered in 1957.

In autumn 1962 it was found in the south-eastern regions of Macedonia (1) which are the principal cotton growing regions of Yugoslavia. There is no doubt that it came to this territory from Greece.

A completely new situation was thus created, requiring research because it was intended that the areas under cotton should be trebled here by 1970.

Fig. 1. Distribution of pink bollworm in Yugoslavia.

The locality at Bar since 1951 has remained a restricted focus.

Immediately after its discovery in Macedonia particular attention has been paid to its spread in this new area. In the course of this inspection 109 samples of bolls from 48 different localities were gathered and 22,296 bolls of cotton were dissected. As a result a map is available of the pink bollworm spread in Macedonia to the end of 1963 showing all the more important localities. These represent in fact the principal cotton growing areas of Yugoslavia (1).

A map of the pink bollworm spread in the world shows that the areas in which this pest has been observed in Yugoslavia represent, with Korea, the northernmost point of the expansion of this insect in the world.

It could be assumed that the population on the northern limits of its natural area of spread in Macedonia would be reduced, to a considerable degree, by abiotic factors. The results of analyses have shown that, if infection by micro-organisms is eliminated (demonstrated by examination of dead caterpillars), very high mortality of caterpillars in the winter 1962/63 was due to low temperatures, which reached in S.E. Macedonia sometimes as low as $-16°C$ and in one locality even $-21°C$.

This hypothesis has been corroborated by the fact that caterpillars, collected in autumn 1963 and deposited in the insectarium for hibernating under natural conditions, had for the most part a successful hibernation in 1963/64 and that the first pupa among these materials was observed on May 6, 1964, outside temperature being as low as $-12°C$. (S.E. Macedonia).

The results of this work have shown that the attack in the new area of spread was economically insignificant, i.e. that the population of the pest was reduced to a minimum. However, it is necessary to point out specially that in some localities there occurred, towards the end of the growing season when already 4/5 of cotton bolls were already picked, a new increase of the population so that in November 1963 the number of attacked bolls was on the increase. In addition to this, in 6 localities there was also an increase of the number of caterpillars per boll, which also corroborates the observation concerning the increase of the population.

In spite of the small number of analysed bolls, the results obtained show that the population of the pink bollworm manifested, towards the end of the growing season 1963, a tendency to increase, notwithstanding the high death rate in the course of hibernating 1962/63.

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MITE POPULATIONS IN FLORIDA CITRUS GROVES BEFORE AND AFTER SEVERE FREEZES

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Citrus rust mite *Phyllocoptruta oleivora* (Ashm.), citrus red mite *Panonychus citri* (McGregor), Texas citrus mite *Eutetranychus banksi* (McGregor) and six-spotted mite *Eotetranychus sexmaculatus* (Riley) are important pests of Florida citrus.

Population sizes for the mites have been recorded each month since 1951. The abnormally severe freezes of 1957-58 and December 1962 presented an opportunity to study effects of cold on mite populations, as background for a pest forecasting service operated by the Citrus Experiment Station.

A trained observer examined the same 5 trees in the same groves every 30 days (1). He inspected 20 outer canopy leaves from each tree, using $2\times$ magnification to scan the entire leaf surface. Population of citrus red mite, Texas citrus mite and six-spotted mite was recorded as percentage of leaves infested with one or more living individuals (eggs excluded). For rust mite, a $10\times$ magnifier was used to observe one lens field (about 1 sq. cm.) on the upper leaf

surface and 1 lens field on the lower surface. If a mite was seen in either lens field the leaf was recorded as infested.

Record was made of grove conditions and details of all spray operations. Groves treated with a miticide in the past 30 days were not included in the computation of population size.

Freeze Periods: The winter of 1957-58 produced a severe freeze (December 12-14) that nearly defoliated 6 of the 130 survey groves. Lesser freezes on January 9, February 4, 5 and 14, were followed by weather favorable to tree recovery.

The winter of 1962-63 produced one very severe freeze December 11-14 (min. temperature 17-23°F) which completely defoliated 66 of the 130 groves. Recovery conditions were good but badly frozen trees did not recover even a reduced canopy of healthy leaves until June. Two groves were destroyed.

Results and Discussion: Conclusions regarding populations were derived after studying per cent of leaves infested and the dates and magnitudes of population peaks before and after the

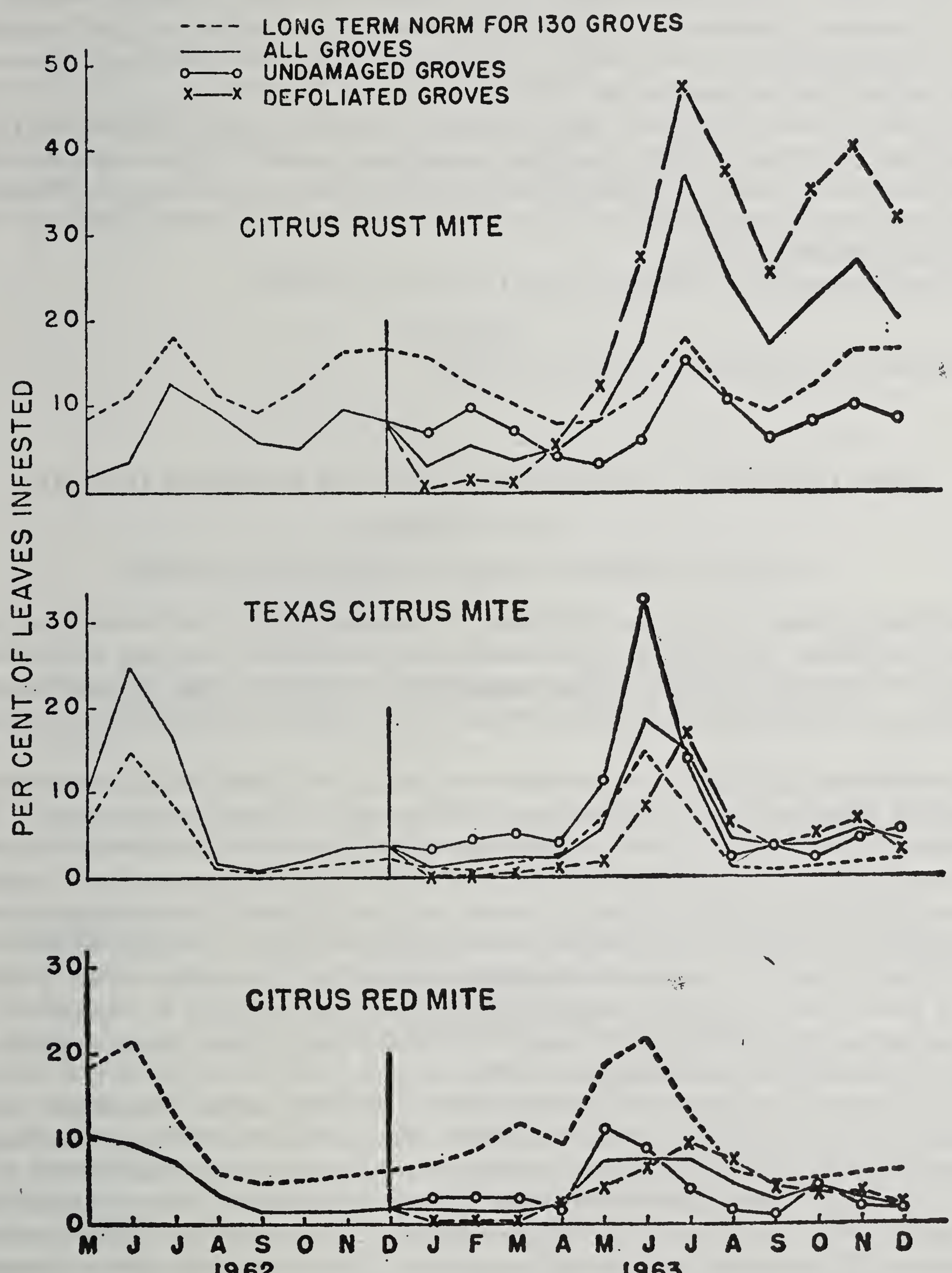

Fig. 1. Populations of 3 mite species in Florida citrus groves before and after the severe freeze of December 1962 as indicated by per cent of leaves infested each month.

freezes. After the December 1962 freeze, records for 64 defoliated groves were compared with 64 undamaged groves (fig. 1).

Citrus Rust Mite: Cold did not kill rust mites directly, but removed them by defoliation. Population was above normal before the 1957-58 freeze and near normal in the year that followed. Population was below normal before the December 1962 freeze and above normal the year that followed. This was attributed to the extremely high population that occurred after May on new leaves put out by freeze defoliated trees (fig. 1).

Citrus Red Mite: Population was slightly below normal before the 1957-58 freezes, continued below normal for 4 months thereafter; then peaked above normal level in June 1958. Statewide populations before and after the 1962 freeze were of similar magnitude; however, in defoliated groves the summer increase of mites was delayed 2 months. Mites were not killed by cold but most of them fell with the abcissed leaves.

Texas Citrus Mite: After the 1957-58 freezes, the summer population was lower and peaked later than in 1957. After the December 1962 freeze, statewide population was near normal. However, summer population in defoliated groves was extremely low for 6 months, then reached a moderate peak one month later than normal. In undamaged groves normal increase to high level occurred at the normal time.

Six-spotted Mite: Population was much below normal in the year before the 1957 freeze and much above normal in 1958. In 1962, population was slightly below normal, and in 1963 was the lowest in 12 years of record. Less than 3% of groves in either the defoliated or the undamaged groups were infested in 1963 and these harbored very light populations. Peaks in all four years occurred in May.

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THE DIVERSITY OF THE ECOLOGY OF MAMMALIAN LICE

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Lice live permanently in the hair-coat of mammals, and breed where and when the physical conditions, particularly microclimatic, for oviposition and egg development and hatching are favourable (2, 4, 6). The populations on each mammal are separate, and vary in distribution and abundance for reasons which differ between species of both lice and mammal.

The southern elephant seal comes ashore on Macquarie Island for 3-5 weeks twice a year yet the hind flippers of most of the seals are infested with *Lepidophthirus macrorhini*. The skin-temperature of the body of the seal is usually determined by the temperature of the atmosphere or sea whereas that of the flipper fluctuates with the seal's thermoregulatory requirements. *L. macrorhini* breeds only when the seal is ashore, and multiplies rapidly on the more-frequently warm flippers (Life cycle—2 to 3 weeks; 8 to 20 eggs laid daily). In the cold sea the louse's metabolic rate is low and cutaneous respiration suffices but a mortality occurs if they cannot feed. A blood meal is required weekly if sufficient are to survive to repopulate the seal. More survive on the hind flipper because of its variable temperature, a rise of which activates the lice which feed before it falls again (3, 7, 8).

The majority of mammalian lice are found on the body rather than on the extremities. On small mouse-like rodents they are usually confined to the head (1). Interference with self-grooming with the teeth permits initially an extension of the distribution of *Polyplax serrata* on the mouse and then an uncontrolled increase in numbers. The grooming technique of the larger rat is less efficient and *Polyplax spinulosa* is more dispersed over the body. Its numbers are still controlled because it has a lower reproductive rate (time to complete life cycle of *P. spinulosa*—3 weeks; *P. serrata*—2 weeks) (5).

The numbers of *Damalinia ovis* on sheep decrease in the spring, remain low in the summer and increase in the winter to ½-1 million in heavy infestations (6, 9). The reproductive rate of

D. ovis is low (life cycle—5 weeks, 1 egg laid every 1½ days, sex ratio 1:1), and, commencing with the usual density of lice found in autumn, 4-6 months are required to produce heavy infestations under optimum conditions. The density at the end of winter is often related directly to that in the previous autumn which is determined by the influence of factors which prevent increases during the summer. Factors such as solar radiation and heavy rain, which may cause repeated slight mortalities, can have severe effects on reduced populations. The behaviour of the sheep in seeking shade or shelter can modify these effects (6 and unpublished).

These examples illustrate—adequate survival for opportune multiplication, great potential to populate small areas controlled by a single factor, and a low potential to populate large areas but successful if initial density is adequate for the time available. They also illustrate how the environments of lice differ between mammals with resultant differences in reproductive potentials which lead to the diversity which exists in the ecology of mammalian lice.

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NATURAL REGULATION OF FIELD POPULATIONS

NATURAL CONTROL OF THE BLACK-HEADED BUDWORM

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Periodic outbreaks of the black-headed budworm *Acleris variana* (Fern.), are relatively common in coniferous forests in North America. Two outbreaks of this species have been observed in northwestern New Brunswick during the period 1946-1963 and limited data, essentially consisting of annual population counts of small larvae and estimates of apparent larval parasitism, were recorded during these two population cycles. A "key-factor analysis" was used to analyse these data and it was found that population changes could be predicted with reasonable accuracy by means of a descriptive equation based on parasitism and weather. Although survival rates within specific age intervals have yet to be defined for this species, it is concluded from the analysis that parasites and weather play a major role in regulating black-headed budworm populations.

SPATIAL FAVOURABLENESS AND PATTERNS OF NUMERICAL CAUSATION

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To change insect pest control from empirical practice into a form of applied ecology demands, amongst other things, a clear formulation of the guiding principles upon which our understanding of population dynamics can be founded. This paper attempts to illustrate that need, and to suggest a way in which some essential notions could be concisely expressed.

In S.-E. Australia, codling moth normally causes each season a virtually total infestation of unprotected apple crops. Interruptions in the measures applied to control the pest commercially allow populations to increase rapidly to damaging densities (1a). In E. Canada, MacLellan (2, 3, 4) has shown that codling moth is generally less injurious, producing smaller populations which increase at slower rates, and can therefore be kept under commercial control at less cost than in Australia.

It was found that the particular procedures of control developed in E. Canada were not applicable with equal success in Australia. An improvement of Australian methods requires therefore an appreciation of the circumstances which determine the relative favourableness of the two regions for codling moth, in order to define what changes are needed to reduce the natural capacity of the Australian environment for the pest.

A first analysis according to standard ecological criteria would show that differences in climate account for the higher rate of seasonal increase observed in Australia, but fail to explain why Canadian populations should not eventually reach saturating densities as they do in Australia. Although weather conditions are less generally favourable for the development of codling moth in E. Canada than in Australia, their variability is such in both regions that they could not consistently enforce and maintain different levels of codling moth densities in each of the two areas (7). As for natural enemies, which MacLellan has shown to play a major role in the ecology of codling moth in E. Canada, they were found to be no less destructive, on the whole, in S.-E. Australia where different species occur.

Thus, no single element of climate, weather, predation and parasitism, nor the comparative availability of requisites such as food and cocooning shelter can be made to account wholly for the differences in the performance of the species between the two regions. To explain the situation in a meaningful way, a unifying concept is required which would link each of the contributing elements into a functional chain, or system, of causative events. Such a concept has been proposed in the term "life-system", defined as follows:—

A life-system is the outcome of the complex functional relationships between the attributes of a species, represented by *populations* (1), and the qualities of the local habitats which form the *effective environment* of the populations. A life-system is a prerequisite for continued existence. It ensures the regulation (10) of population densities. The concept is derived from Tansley's ecosystem (9). Whereas ecosystem refers to the sum total of functional relationships occurring throughout a *community* of different organisms living together in a given space, life-system includes solely those elements of an ecosystem which bear *significantly* upon the life of one kind of organism considered as the *subject species*, in this case codling moth. In the life-system, neither populations nor environments are taken as entities in their own right, but as constituent elements of the system, defined for convenience of purpose, and mutually dependent for their existence. Thus, one would prefer not to say, like Milne (5): "the environment rules"; or like Nicholson (6): "populations are self-governing systems"; but rather: "the life-system rules", and "life-system governs", for it is felt that the two statements cited, although not incorrect in their proper context, require too much qualification in current usage to avoid evoking misplaced emphasis on particular factors involved in the determination of animal numbers.

The life-system of a species cannot be delimited in space and time according to absolute criteria, any more than other ecological concepts. The extent to which the life-system must be taken is a matter of relevance to the purpose of one's study. In the present instance, the life-system of codling moth would be analysed only to the extent required to effect substantial improvements in current methods of control.

In S.-E. Australia, favourable conditions of climate and weather allow the codling moth to produce very high numbers of individuals relatively to resources in food and shelter, despite

the action of natural enemies. At those densities, populations are *stabilised* by two complementary mechanisms, each involving a form of intraspecific competition. The first is contest (6) amongst larvae for food and space in fruits. The second is competition amongst mature larvae for accessible overwintering sites in which to spin their cocoons.

In E. Canada, climate and weather patterns present a less favourable environment for the pest. Consequently, the reduced rate of increase in codling moth enables natural enemies to stabilize populations at levels well below those at which supplies of larval food and of cocoon shelter become seriously depleted. Factors such as competition for prey amongst natural enemies and variations in numbers of alternate prey probably contribute to making stabilization less rigid than under Australian conditions, although the expected variability in the action of single species of natural enemies appears to be reduced by compensatory or substitutive effects in the concurrent actions of different predatory agents.

Thus, codling moth reveals two very distinct life-systems in S.-E. Australia and in E. Canada. In the former, densities are high, intraspecific competition normally becomes acute each season, and stabilisation of numbers is achieved by *adjustment* of population densities to the availability of two requisites, larval food and cocoon shelter. In the latter, densities are naturally lower, and stabilisation is achieved by *containment* of population numbers, through the action of natural enemies, at levels which do not normally result in the depletion of requisites.

Stabilisation by *adjustment* is constant and rigidly enforced by the automatic nature of the mechanisms involved. Stabilisation by *containment* may be looser, and apt to vary in effectiveness because the mechanisms that implement it involve elements whose qualities are not solely determined by those of the subject species.

These views are not presented as original ideas, nor are they intended to refute or replace the more elaborate conceptual models. They are meant to propose a brief and flexible expression for some working concepts in applied ecology. The subject is treated more fully in papers submitted to the Australian Journal of Zoology by L. R. Clark and by the present author.

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THE ANALYSIS OF FACTORS AFFECTING REPRODUCTION AND MORTALITY IN A NATURAL POPULATION OF THE PINE LOOPER, *BUPALUS PINIARIUS* L.

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Many phytophagous insects fluctuate in numbers well below the carrying capacity of their food plants. It is often assumed that this must be due to the regulating influence of parasites and predators. Evidence is presented suggesting that in the pine looper numbers are most probably regulated through mutual interference between larvae.

Eggs are deposited on needles of Scots pine on which the larvae live from mid-June to mid-October. When full-grown they fall off and pupate beneath the moss. Adults emerge in May-June. One female deposits about 175 eggs in small rows of 3-8, distributed at random on the trees.

Population density has been measured at all stages from egg to adult. Some measurements can be expressed directly as number per sq. m., others are related to surface area via twig mass (1 and 2). Density measurements and rearing results enabled us to compose life-tables (fig. 1—very condensed).

Analysis of mortality. Mortality has been analysed by making use of the key factor method (3). The generation mortality graph (fig. 2) shows marked fluctuations. If mortality is higher than 99·54% density decreases, if lower than this then there is a population increase, as shown by comparing fig. 2 with fig. 1 (upper graphs). The fluctuations are governed by those factors whose mortality graphs show the best fit to the generation mortality graph. It appears from fig. 2 that the mortality occurring prior to the pupal stage is responsible for the changes in size of generation mortality, whereas factors operating in a later stage have very little effect. The first group of factors is composed of a very heterogeneous complex including both biotic and abiotic agents.

None of these factors showed a significant correlation with density when plotted against the initial number of the stage upon which they operate. This indicates that insect numbers are most unlikely to be regulated by a relatively simple direct density dependent mechanism. Moreover, parasites do not play a significant role in regulation (fig. 2).

Fig. 1 shows that there is a general tendency for the mortality from egg to larval stage (including both egg and first instar larval mortality) to be high or low after a high or low larval density in the previous year respectively. If this interpretation of the facts is correct, this remarkable relationship might have far-reaching consequences from the viewpoint of population regulation. Since this is not obvious, however, it calls for further explanation (see below).

Analysis of reproduction. A large sample of pupae was taken at random each winter and nonparasitised pupae selected and measured. There was a noticeable variation in mean pupal size between years, which could not be shown to be due to the weather. Pupal size in winter, however, proved to be negatively correlated with the larval density of the previous summer (fig. 3). This relation is highly significant ($\tau = 0{\cdot}70$; $P = 0{\cdot}002$).

This inhibiting effect of high larval density on larval growth, resulting in small pupal size, has been studied in simple experiments, in which larvae were reared singly, in couples, and five by five in jars of 0·37 l. contents, with plenty of fresh food. The results were quite conclusive in both sexes, as shown for females in table 1.

TABLE 1

	Mean pupal diameter (mm)	*Standard deviation of mean*	*Number measured*
Larvae reared singly	5·38	0·03	50
in couples	4·98	0·03	47
five by five	4·86	0·06	19

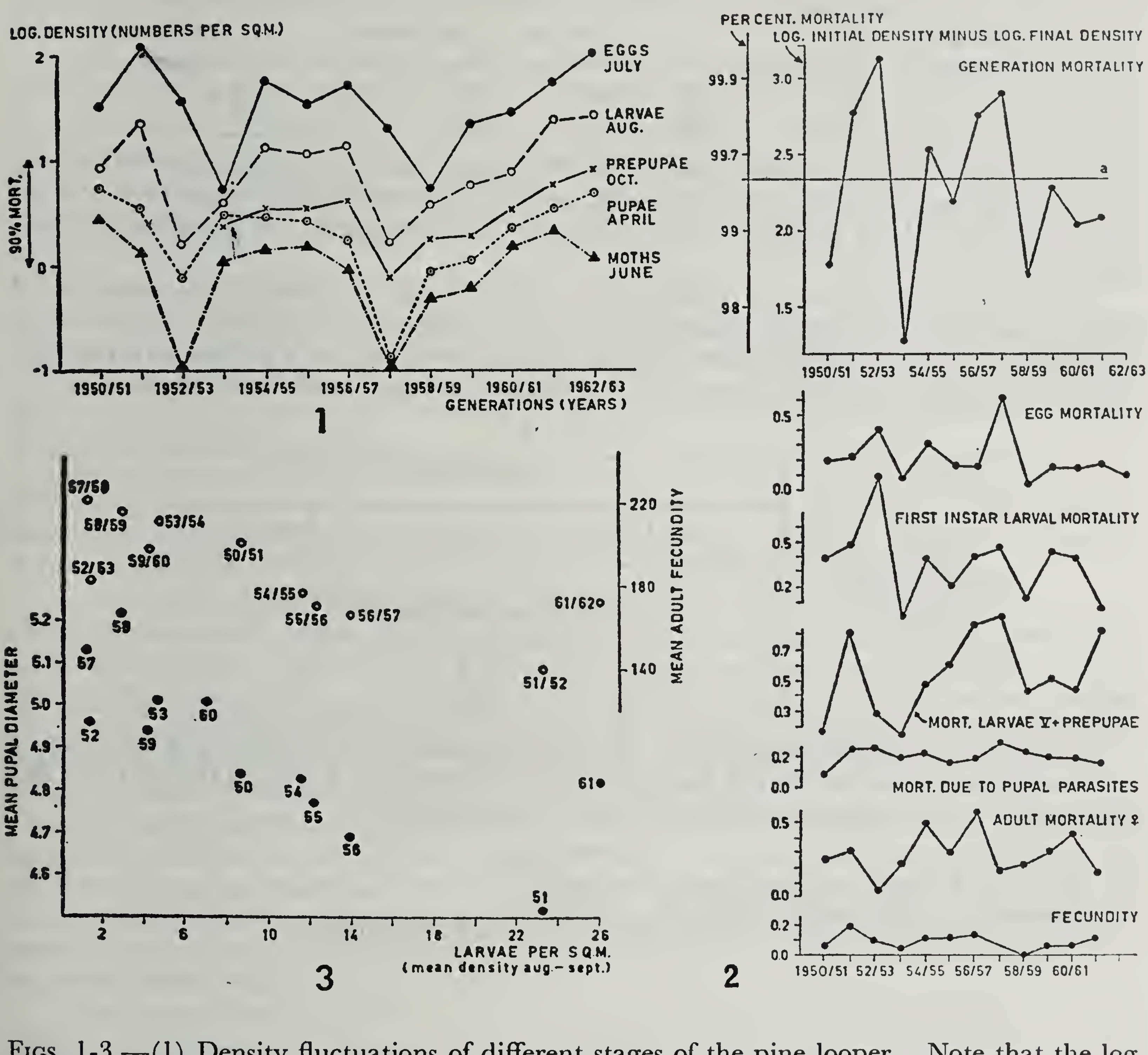
The experimental density of two larvae per jar exceeds the highest density ever experienced by us in the field. It is of great importance therefore that a similar effect could be shown to exist in the field after the creation of artificial differences in larval density within the natural range between adjacent trees in the same season.

Rearings show that female fecundity is positively correlated with pupal size. Consequently, a combination of these relations leads to a density dependent fecundity (upper graph fig. 3). This relation is significant ($\tau = 0{\cdot}67$; $P = 0{\cdot}005$) (Kendall's rank correlation).

Two important questions now arise. That concerned with the causation of the density effect among larvae will be considered no further in this contribution, but we can emphasise here only that competition for food can be excluded as a causative process. The other question refers to the significance of the density dependent reproduction in the population dynamics of the moth. Relying on the degree of the reduction in the fecundity at the higher densities, amounting to 25%, one is inclined to credit the relationship with a relatively great regulatory effect. There are several arguments, however, which can be advanced against this viewpoint. One of these will be given here because it can be elucidated from the figures 1 and 2. In general, regulation might be expected to be in operation when the population declines after

having reached a high level, or increases sharply after a very low level. As can be seen in fig. 2, the density induced variability of fecundity in these cases is far from being a predominating factor in the complex of agents involved in the density changes.

Density and viability of progeny. Larval density thus affects growth directly and pupal size and adult fecundity indirectly. If larval density were to have an additional influence on the viability of the eggs and first instar larvae of the next generation, then the relationship between larval density and mortality from egg to larval stage referred to above could be explained. This point has been studied experimentally by breeding eggs and young larvae of singly and



Figs. 1-3.—(1) Density fluctuations of different stages of the pine looper. Note that the log scale enables a direct reading of per cent. mortality between stages, e.g. in 1952/1953 the mortality between egg and larval stages amounts to more than 90%, in 1953/4 it is less than 20%. (2) Comparison of some submortality curves with generation mortality according to the key factor method of Varley and Gradwell (1960). Generation mortality has been computed as log (egg density) minus log (surviving moth density), egg mortality as log (egg density) minus log (first instar larval density), etc. Fecundity has been treated as a mortality factor, by taking the difference between log maximum fecundity (216 eggs per female, found in 1957/1958) and log actual fecundity of a given year. (*a*) indicates per cent. mortality in the steady state, which can be computed as log (maximum fecundity) minus log (moth density in steady state) = log 216–log 1 = 2.33, if the percentage males is also treated as a mortality factor (not presented in this figure however). (3) Diagrams showing the effect of larval density on mean pupal diameter • and on adult fecundity ∘ in a field population of the pine looper. The numerals refer to years.

gregariously reared parents. When the eggs of such parents are reared under a variety of constant environmental conditions, the two groups show clear differences in hatching success as shown in table 2, these being most pronounced in the extreme treatments.

TABLE 2

	Treatment of eggs						
Temp (°C)	28°	28°	25°	15°	10°	< day 30° / night 4°	
R.H.	23%	75%	75%	75%	75%	75%	—
Parent larvae per jar	Per cent. of eggs hatched						
1	14	76	86	90	49	78	
5	2	46	60	61	15	53	

In all treatments the batches consisted of 240-350 eggs, laid by approximately 30 females. The eggs were kept permanently in the dark, except in the last column where 18 h. of light alternated with 6 h. of darkness. All differences within treatments are statistically highly significant.

If larvae, hatched under the conditions of 15 and 25°C given in table 2, are reared under outdoor conditions the parental groups do not show any difference in viability. Under conditions of stress (1 or 2 days of starvation immediately after hatching), such differences do appear, as shown in table 3. The differences within treatments are once more highly significant.

TABLE 3

	Starvation	
	1 day	2 days
Parent larvae per jar	Per cent. survival after 10 days	
1	62	21
5	13	5

This shows clearly that larval density does have an influence on the viability of the offspring in the next generation, but we still have to provide the proof that density in the field is in fact regulated by this principle of mutual interference among larvae.

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MODIFICATION OF THE NATURAL REGULATION OF APHIDS BY LOCAL CLIMATES IN CALIFORNIA

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Populations of aphids and their parasites, predators and pathogens were studied in a series of alfalfa fields distributed through several climatic districts of middle lowland California. These populations were studied throughout the year in 51 alfalfa fields and in many for several consecutive years. The local climate of each field was also assessed in terms of relative humidity, temperature and rainfall. Supplemental detailed studies were made of incident radiation and the microstratification of temperature and humidity.

The climatic districts varied from the cool, moist, stable conditions of the coastal areas to the hot, dry, continental conditions of the interior valleys. As would be expected, these varied

conditions affected the alfalfa, the aphids and the natural enemies of the aphids, but not all in the same pattern.

The pea aphid, *Acyrthosiphon pisum* (Harris), and the spotted alfalfa aphid, *Therioaphis trifolii* (Monell), are the only species of importance in alfalfa and both are introduced. In general, the spotted alfalfa aphid is a warm-weather aphid and is favoured by the weather conditions prevailing in the interior valleys from May to September. In contrast, the pea aphid is a cool-weather aphid favored by spring conditions in these areas. The most significant aphid predators are native coccinellids which vary in species composition among the climatic districts. Other aphid predators including chrysopids, geocorids, syrphids, and nabids are erratic in occurrence and usually their predation is merely a contribution to the dominant role of the coccinellids.

The parasites are all rather recent introductions of species belonging to the genera *Aphelinus*, *Praon*, and *Trioxys*. In the early years of these investigations, the introduced parasites were not present. They have now become important regulatory agents and have supplemented the biological control afforded by the native predators by being active particularly during the summer months. *Entomophthora* is important under some special conditions. Alfalfa varieties resistant to the spotted alfalfa aphid are now commonly grown and this also influences the general abundance of that aphid. The cultural practices of harvesting and irrigating alfalfa maintain an almost continuous supply of suitable plant tissue for the aphids for most of the year. In summer, in the hot interior areas, there is considerable aphid mortality and movement between fields in the immediate post-harvest period. Pre-harvest emigrations of aphids triggered by aphid density or plant condition are not a common occurrence. However, where chemical treatments have disturbed natural regulation such emigrations can occur in the presence of high aphid densities.

Not all species of aphidophagous coccinellids occur in all fields at the same time. The *Hippodamia* species with facultative imaginal dormancy are more sensitive to aphid presence, responding reproductively if sufficient aphids are present. *Coccinella* species all enter an obligate aestival dormancy, therefore do not react to summer aphid abundance.

The climate of the extreme coastal area is favorable for pea aphid development and reproduction through most of the year, but is generally too cool for significant spotted alfalfa aphid reproduction. The main predator species is *Hippodamia parenthesis*. *Coccinella californica* and *C. trifasciata* are favored in the spring but are not functional during the summer months when aphid populations are highest. This area is too cool for *C. franciscana*. Conditions in the coastal areas can be so cool as to prevent feeding and reproduction of the predators, but warm enough to permit a slow increase in the pea aphid populations.

The middle coastal areas are near the limits of influence of summer fogs. These areas have the greatest number of coccinellid species in alfalfa. *Coccinella californica* and *C. franciscana* reach their greatest abundance here and are effective in the development of the spring crash in the aphid populations. Nevertheless, the *Hippodamia* species are still the dominant mortality factors. Aphids have the potential to develop to economic levels from April to October, but the action of the predators prevents this in nearly all instances.

The Central Valley provides cultural and environmental conditions favorable to the pea aphid in the spring and fall and to the spotted alfalfa aphid from late spring to early fall. *Hippodamia convergens* and *H. quinquesignata punctulata* are the most common and most important aphid predators in alfalfa fields of these areas. They dominate the predator complex that develops on the spring populations of aphids. This predator complex produces a crash in the aphid populations at a variable date in the late spring. The timing of this crash in each field is influenced by weather, harvest timing, and the size of the aphid populations. The severity of the crash influences cannibalism of the predators and the initiation of the facultative summer diapause in the *Hippodamia* populations. *H. convergens* that do not find adequate numbers of aphids leave the alfalfa areas to aestivate and hibernate in the mountains. Most of the individuals of this species are out of the alfalfa area for the next nine months. Aestivating *H. q. punctulata* remain in the valley and may react to presence of fall aphid populations. The rapidity of summer resurgence of the spotted alfalfa aphid is apparently dependent upon favorable temperatures and from what base level the increase begins after the crash caused by predation. Low populations of *Hippodamia* that do not enter diapause can survive on low

residual aphid populations and often maintain sub-economic levels of aphids for several months.

Where several species of coccinellids occur together in the Central Valley, *Hippodamia convergens* and *H. q. punctulata* are best adapted to the aphid complex in alfalfa. The *Coccinella* species drop out because of their obligate summer diapause. The other species of *Hippodamia* do not compete as well but the precise reasons are unknown.

In summary, the aphidophagous coccinellids have moved into the alfalfa ecosystem from their native spring-grassland habitats and have assumed a dominant role in natural regulation especially in the spring and fall. The precise role and species composition of the coccinellids is greatly influenced by local climate.

FACTORS OF POPULATION DYNAMICS OF *EURYGASTER INTEGRICEPS* PUT. IN DIFFERENT PARTS OF ITS RANGE

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A study of population dynamics of *E. integriceps* was carried out during 7 years in the regions of outbreaks of this pest (North Caucasus, Saratov region), as well as at the sites where its population density was stably maintained at a low level (Armenia). Population trends of the pest were compared with its morpho-functional state, meteorological conditions, phenology of its food plants and with the activity of its natural enemies.

In the regions with a stable low population density the morpho-functional state of *E. integriceps* is not inferior to that at the sites with chronic outbreaks. Alterations in fecundity do not always coincide with the population trends, although they exert a certain effect on trend index.

The direct action of abiotic factors during *E. integriceps* development has no decisive importance, which may be illustrated by several facts of a more intensive propagation of the pest in the years with less favourable weather conditions.

The main food plants—winter and summer wheat—provide the termination of the development of the great part of the *E. integriceps* population. The adult bugs are able to feed additionally on ripened grain on cut crop and to migrate to later ripening crops (oat, millet). All this ensures high survivability of the pest even in case of an early harvest.

The maximal mortality of *E. integriceps* is found at the egg stage and perhaps, in 1-2 instar larvae and depends mainly upon the activity of egg-parasites. Female castration by the parasitic flies of the subfamily Phasiinae is added to this. In different parts of *E. integriceps* range the trend index reveals a distinct dependence upon the activity of the above mentioned groups of natural enemies.

The complex of parasites of *E. integriceps* is different in different parts of its range. In the optimal zone with a low mortality from abiotic factors (North Caucasus) it includes along with polyphagous forms (Scelionidae, *Ectophasia crassipennis*, *Helomyia lateralis*) also more specialised parasites (*Clytiomyia helluo*, *Phasia subcoleoptrata*). At the sites with a high winter mortality (Saratov region) the specialised Phasiinae species are absent, and the polyphagous *E. crassipennis* has insignificant importance for the population dynamics due to the late infection of hibernated bugs and the high immunity (up to 70%) to it by the young females.

In several regions of Armenia the population density of *E. integriceps* is retained at a very low level (0·03-0·28 specimens per 1 m^2). The trend index here has a distinct reverse dependence on population density, which bears witness to a sufficiently perfect regulation by reactive biotic factors.

A comparison of the conditions of existence of *E. integriceps* in different parts of its range demonstrates that the main cause of chronic outbreaks of this pest is the impoverishment of communities in the main grain farming regions of the U.S.S.R., which creates deficit of alternating hosts and hibernation sites for parasites.

Intense chemical control does not contribute to a depression of the population density. The treatments against hibernated bugs lead to a sharp decrease in the effectiveness of parasites. At the same time they often result in considerable mortality (40-60%) of hibernated bugs.

THE NATURAL REGULATION OF THE POPULATION OF THE SOUTHERN GREEN STINK BUG, *NEZARA VIRIDULA* L.

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The distribution of *Nezara viridula* in Japan is marginal from the viewpoint of world distribution, and it is found only in the south (8). Its polyphagous habit implies diversity of habitat, importance of timing between host plants and the life cycle of the insect (4). Multivoltinism and long oviposition period of overwintered females result in a complex age structure and an overlapping of successive generations (2).

A dozen life tables showed that the total mortality up to the adult state exceeded 94%, and the mortality from egg to third instar was 70 to 95% (5). Key factor analysis (7) revealed that mortality by the end of the second instar determined the level of total mortality and the former was determined by the egg mortality caused by parasitism. However, percentage parasitism showed no relationship to egg-mass density mainly due to differential ability of dispersal between host and parasites (3).

Recent increase of *Nezara* in southern Japan has been induced by early planting of paddy (8, 9) which provided a suitable site for feeding and oviposition when other host plants were scarce (4, 5). The mosaic distribution of early as well as late paddy within a given area often induced a local overpopulation by the concentration of eggs on rice in the milk stage which is suitable for feeding and oviposition. Experiments showed that mortality during immature stages increased, while longevity, body weight and fecundity of the adults were reduced with increase of egg density. These effects are considered to be the key process which checks a further increase of population.

When relative abundance and seasonal combination of host plants are fixed, abundance of the bug is determined by climatic conditions. Warm conditions from Sept. to Dec. increased the density of pre-hibernating populations by producing adults of a fourth generation (2), though most of them died of malnutrition during the winter. The severe winter in 1962-3 gave 97·5% mortality, but the heterogeneity of hibernacula prevented them from dying out. More females than males survived during the winter probably due to physiological difference between the sexes (2, 6).

Mortality factors work in a stage-specific way, i.e. parasites against eggs, weather factors against the first instar and predators against the second (1, 3, 5). Evidence obtained under natural conditions suggests that the complex age structure during the breeding seasons increases the population plasticity against a specified mortality factor.

It was concluded that the upper limit of the population density of *Nezara* is determined by the deleterious factors associated with overpopulation which occurs locally due to the relative shortage of food. The elimination of *Nezara* population is prevented by the heterogeneity of both environment and population.

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DYNAMISME DE LA POPULATION *PROSPALTIELLA PERNICIOSI* HOW., ELEVE SUR LE POU DE SAN-JOSE (*QUADRASPIDIOTUS PERNICIOSUS* COMST.), DANS LA CHAMBRE ACCLIMATISEE

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Methodes de Recherche. Pratiquement, il est difficile de faire des recherches de cette sorte sur des citrouilles entières envahies par le Pou de San-José, et sur lesquelles on élève *P. perniciosi.* Nous avons essayé de résoudre cette question d'une autre manière.

Dans ce but, nous avons choisi une citrouille sur laquelle avait été commencé l'élevage de *P. perniciosi*, le 26.I.1961, dans la chambre acclimatisée à 27°C et 70% d'humidité relative. Trois carrés d'une surface de 5 × 5 cm. y ont été ensuite mesurés. Autour de ces carrés les boucliers ont été nettoyés sur une largeur de 1·5 cm. De cette manière, chaque surface de 25 cm² représentait, en petit, une population, composée de *P. perniciosi* et de son hôte, le Pou de San-José, c'est-à-dire que sur la citrouille étaient isolées trois populations de densités différentes A-B-C. Ensuite, sur chaque surface ainsi préparée nous avons posé un cadre de carton noir, dont la base était accommodée au relief de la place en question sur la citrouille, sur laquelle il était fixé par une bande collante; puis l'espace se trouvant entre cette boîte et la citrouille a été enduite de paraffine liquide, ce qui a permis d'obtenir l'isolation complète de la surface determinée. Sur la partie supérieure du cadre a été placée une feuille de celophane qui était régulierement enduite de glu sur sa face inférieure. Sur une surface ainsi isolée *P. perniciosi* a été élevée; ses adultes, après leur éclosion, étant donnée leur photophilie marquée, volaient et se collaient sur la cellophane transparente. Celle-ci a été enlevée tous les jours et les adultes de *P. perniciosi* ont été comptés au binoculaire.

Resultats du Travail. Le contrôle journalier de l'apparition de *P. perniciosi* a été fait du 8.III.1961 au 22.I.1962., soit pendant 321 jours, et l'élevage du Pou de San José a commencé depuis l'automne 1960 jusqu'au 26.I.1961.

Les resultats de cette expérience montrant le dynamisme des éclosions de *P. perniciosi* dans une période determinée et d'une population de densité déterminée, sont indiqués sur le graphique 1, et permettent d'en tirer les conclusions suivantes:

1. Il y a une corrélation marquée entre la densité de la population de l'hôte et la densité de la population des adultes éléves du parasite.
2. Le rapport numérique des parasites éléves dans des populations choisies de l'hôte a été du plus dense au plus rare, comme ceci: A = 1345, B = 724 et C = 231, ce qui fait pour les trois populations un total de 2,300 adultes élévés de *P. perniciosi.*
3. D'après ces données on peut compter qu'une population moyenne sur une surface de 25 cm² s'éléverait à 766 adultes.

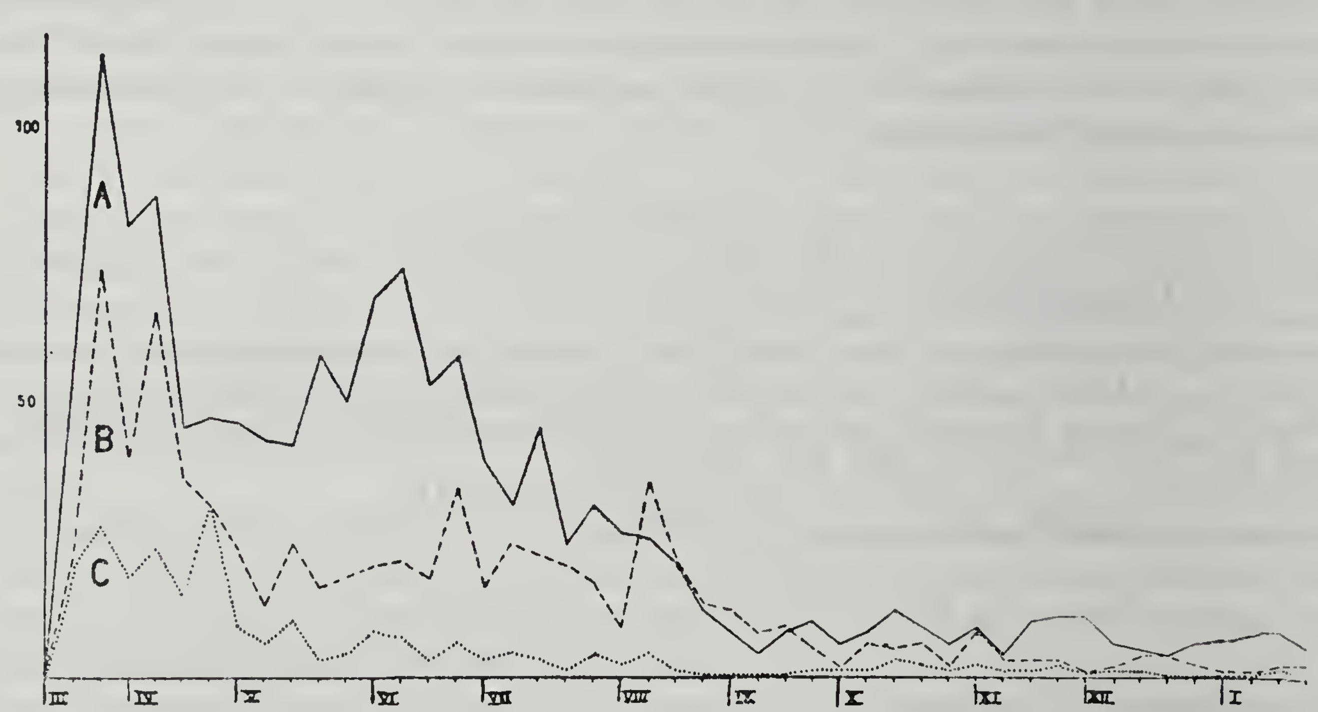

Fig. 1. Dynamisme des éclosions de *P. perniciosi*.

4. Le graphique (fig. 1) montre nettement une diminution de la densité de la population de *P. perniciosi* sur les trois surfaces isolées. Ce phénomène peut s'expliquer par la photophilie des adultes de *P. perniciosi*, c'est-à-dire, qu'après l'éclosion, ils se dirigent en grand nombre vers la source de lumière ou ils se collent et périssent sur la celophane transparente avant la ponte, d'ou la diminution progressive de la population.

L'importance de cette expérience repose dans le perfectionnement de la possibilité d'estimer le plus exactement possible la densité de la population de *P. perniciosi* sur les citrouilles qui sont placées dans la nature. Afin d'obtenir des données approximatives pour cette estimation, seules ont été prises les données sur l'éclosion de *P. perniciosi* pendant les premiers 60 jours, soit du 8.III.1961 au 7.V.1961, car c'est là ce qui correspondrait d'une part à la vie moyenne d'une citrouille, et d'autre part, à la population de *P. perniciosi* qui abandonne le Pou de San-José sur la citrouille. Cela s'éléverait dans l'expérience décrite, comme suit: A=561, B=326, C=158; T.1045, soit en moyenne 348 adultes de *P. perniciosi* sur 25 cm^2.

Pour ce calcul, il faut partir de la surface de l'ellipsoide, la sorte de citrouille employée ayant en général une forme ellipsoïdale. Comme base de calcul, c'est le nombre moyen qui servira, soit 348 adultes de *P. perniciosi* sur la surface expérimentale de 25 cm^2 ce qui signifie, que sur 1 cm^2 il y a 13·9 adultes du parasite pour une periode de 60 jours. Il en ressort que, pour la même période sur la surface entière de la citrouille, 73·368 adultes y seraient éléves, et qui seraient lâchés en liberté dans la nature, lorsque la citrouille serait portée dans le verger.

INTERPRETING WINTER MOTH POPULATION CHANGES

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The winter moth (*Operophtera brumata* (L.)) has one generation a year. A census of larvae and of adult females on oaks in Wytham Wood, near Oxford, has provided life tables for the years 1949 to the present.

Different mortality factors act successively on different developmental stages. When their killing powers are expressed on a logarithmic scale as "k-values" (the difference between the logarithms of the densities before and after the mortality) they can be added to give the total mortality "K" for each generation. Plotting the individual k-values for a series of years gives a graph which conveniently and simply expresses much of the useful life-table information; comparing the shapes of the curves with a plot of the Ks shows the contribution of each separate part of the mortality to the total. From such a graph we identified "winter disappearance" as the key-factor mainly responsible for population change and suggested that "pupal predation" tended to compensate for changes caused by the key-factor (1). Later we demonstrated that pupal predation was a density dependent factor which appeared to have a weak delayed component (2).

We developed a mathematical population model to investigate the interactions of a randomly variable key-factor, a specific and synchronised parasite with a fixed area of discovery and a density dependent factor (3), (4). This model helped considerably to explain the roles of the various types of mortality, and produced population fluctuations comparable with those observed in the field.

The key-factor, winter disappearance, is composite. A major part of it arises from the failure of newly hatched larvae to establish themselves in the partly opened oak buds. This mortality is probably influenced by weather in a complex way that we do not understand and we cannot yet predict its changes. If and when this key-factor is predictable the population model should not only explain the mean population level but also predict both population changes and the results of any insecticide treatment.

We have applied the procedures suggested by Morris (5), (6) for key-factor analysis to our

results but have used k-values instead of his peculiar logarithmic transformation of survivals which are statistically equivalent. The analysis gives a highly significant relationship ($p < 0{\cdot}01$) between winter disappearance and total K and less significant relationships ($p < 0{\cdot}05$) between the k-values for parasitism by the Tachinid fly *Cyzenis albicans* and the Ichneumonid *Cratichneumon culex* and total K; it does not reveal that pupal predation has any interesting relationships.

The reason why these two different procedures produce different answers from the same information is that they are designed to look for two different things. We seek to produce a population model whilst Morris seeks a mathematical formula which will predict the population density one generation ahead. In effect Morris's method is to test statistically the relationship between each of the k-values and total K. This is a logical mathematical procedure to adopt in order to find which mortality varies in a similar way to, and thus permits prediction of, the generation mortality, but the results obtained from such an analysis do not necessarily have any biological meaning; thus although there are statistically significant relationships between total K and the mortalities due to parasites, these relationships cannot be causal because of their great difference in magnitude.

Morris's method of carrying out a correlation of the parts on the whole and always summing his log. survivals from egg to egg does not necessarily identify the factor which is most likely to prove useful in the prediction of the population density of stages other than that of the egg. If the mortality egg to larva is variable and, as in Morris's examples, it is required to predict the larval density, it would seem reasonable to make a regression analysis on the basis of a generation running from larva to larva; using the same individual log. survivals (or k-values) the total survivals will be quite different and thus the statistical results of the analysis depend on the generation period selected.

We can illustrate this with a second key-factor analysis of our figures, summing the k-values from larva to larva. There is now no correlation between mortalities due to parasites and K; winter disappearance continues to be correlated with K but its apparent predictive value is less ($p < 0{\cdot}05$, $> 0{\cdot}01$) than in the first analysis and pupal predation ($p < 0{\cdot}01$) is now shown to be the mortality most useful to the mathematical prediction of next year's larval density.

When we graph the k-values and total K from larva to larva we can see that there may be difficulties in attempting to identify biological mechanisms from the type of key-factor graph we have used previously. In the graph of our second analysis pupal predation varies in a similar way to the key-factor acting after it, so it appears to contribute to population variation and not to its stability.

Difficulties in interpreting a key-factor graph probably arise because we have variations in mortality partly compensated by density dependent mortality. Since most populations fluctuate about a fairly stable mean level, the inference is that density dependent mortalities will be found to act on most populations and that such difficulties will be general.

We can see no biological mechanism by which mortality factors can be affected by the percentage mortality caused by earlier, or later acting factors; they can react only to the present population density. We therefore suggest that the initial analysis, irrespective of whether the requirement is a model or a predictive equation, should be a regression analysis of the individual k-values against the log. population density on which they act. If these regressions are expressed graphically and the points are linked serially it is possible to identify direct density dependent factors, inverse density dependent factors, delayed density dependent factors and key-factors which may vary independently of density. It may be necessary to apply more refined statistical tests to prove the relationships suggested by the curves.

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A DENSITY DEPENDENT ACTION IN NATURE AND FACTORS TENDING TO OBSCURE ITS EXPRESSION

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Density dependent action is the factor which enables entomophagous forms to control (i.e. govern the density of) their hosts. It follows that density dependent action is a keystone of biological control.

Studies of the interrelationships of the pea aphid, *Acyrthosiphon pisum* (Harris) and its parasite *Aphidius smithi* Sharma and Rao in alfalfa in Southern California clearly revealed the density dependent nature of the parasite. This is of particular significance because clear cut examples of density dependent action in nature have been rare.

The Southern California studies were conducted at Riverside, Riverside County from July 1961 to July 1962 and at Pala Mesa, San Diego County from July 1962 to July 1963. The plots were sampled twice weekly with a De Vac Mechanical Sampler, the collected material being processed through a modified Berlese apparatus. As a result of this activity abundant data were obtained from two intensively sampled plots separated in time and space. Critical phenomena revealed by the Riverside study were essentially corroborated the next year in the Pala Mesa study.

The density dependent nature of *A. smithi* was particularly well demonstrated because the multivoltinism and short life histories of both host and parasite resulted in a repeated manifestation of the phenomenon.

The demonstration of *A. smithi's* density dependence in nature is in itself important. However, the revelation of the obscuring effects of a complex of environmental factors on the parasite's density dependence is felt to be of even greater significance. The masking effects of the environment on the density dependent nature of entomophagous forms probably accounts for much of the confusion that exists as regards the significance of this phenomenon in the regulation of insect abundance.

Factors which tended to obscure the density dependence of *A. smithi* were, (1) the alfalfa harvesting practice, (2) apparent lethal effects of high summertime temperatures on the wasps, (3) apparent adverse effects of low wintertime temperatures on the wasp's sex ratio and (4) competitive superiority of fungus disease over the wasp in simultaneously affected aphids.

These interfering factors tended to obscure the density responsiveness of *A. smithi* over most of the year. Significantly, though, in both studies during late spring when climatic conditions were optimum, competition from fungus disease at a minimum, and hinderance from alfalfa harvesting not a factor, the parasite clearly responded to increasing host density and overwhelmed the aphid population in short order.

Thus in both studies situations occurred in which *A. smithi's* density dependence was, (1) completely masked as by the combination of alfalfa harvesting and high temperature in summertime, (2) partially masked as by competition from fungus disease, and (3) fully manifested as in the late spring devastation of the rising aphid population.

We can see, therefore, that an entomophage (in this case *A. smithi*) works within an environmental framework which, depending upon time or place, may not at all obscure, may partially obscure, or may totally obscure its fundamentally density dependent nature. However, no matter which of these situations prevails it does not alter the fact that the entomophage is essentially density dependent and will under optimum conditions clearly manifest this characteristic.

INTRASPECIFIC COMPETITION FOR FOOD: THE ROLES OF DISPERSION AND SUPERIMPOSED DENSITY-INDEPENDENT MORTALITY

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The present laboratory study of a single species of phytophagous mite permits us better to appraise the roles of various factors in complex natural communities. The interplay between simple intraspecific competition for food, the regulating factor, and the complex and varying *conditioning* factors employed illustrates and emphasizes the inseparable, mutually compatible aspects of these two basic classes of factors in explaining natural control of populations in communities. Many kinds of species in communities compete for the same things, very often for food, and this, sometimes in inapparent ways. Food is dispersed variably in environments and its utilization is often not only a function of the dispersion, but the process of competitive use itself modifies the quantity, quality and the dispersion, altering availability.

Populations of the mite, *Eotetranychus sexmaculatus* (Riley), were studied under controlled, stable conditions of temperature and relative humidity, while in different universes the dispersion of the oranges as food for the mites was varied, and an additional density-independent mortality was applied weekly in some universes. In addition to the light they shed on natural control, just stated, the results illustrate how competition for food may be limiting for a species even though only a small portion of the available food is utilised.

The concensus for many years has been that phytophagous insects do not commonly destroy their food supply to the point of the resultant shortage serving to limit their abundance. This is contrary to the premise on which the biological control of weeds rests, and since we feel that host-specific phytophagous insects may commonly limit, and be limited by, their plant hosts, we were concerned with the apparent discrepancies.

Furthermore, the idea has occurred often from general field observations that the degree to which favorable habitat units are dispersed in the general environment, may have a marked bearing on the amount of diffusion losses an insect would suffer in relation to the rewards of realisable reproduction. Moreover, the intensity of such losses, even if entirely unrelated to density, would be expected to *alter* the level of density at which the true regulating factor would govern the population's *characteristic* abundance. Now, if in fact a low intensity of action of a regulating factor is all that is required to balance births and deaths when a high level of such diffusion losses or other density-independent stresses are suffered, then the population can only reach a relatively low density commensurate with the low intensity of action required of the regulating factor.

It is also most significant that the importance of the regulating factor, *as a regulator*, cannot at all be appraised simply on the basis of its sometimes quantitatively low intensity of action, as for example when causing a low mortality. Very low mortality under one group of conditions may be just as crucial as high mortality under others! It thus seems to us incomprehending to think that density-dependent actions only come into play at high densities while density-independent actions have the major role at lower densities.

The present results help to explain these interdependent complexities. In these experiments two techniques were used to alter the degree of density-independent stress, while competition for food remained the only *regulating* factor. First, in some of the different ecosystems a different spatial dispersion presenting different hazards to movement was used in respective systems. Secondly, in another group, a "standard" design of spatial dispersion was used, and varying fixed levels of weekly destruction of the mites were applied or superimposed.

Table 1 presents the summarised data and explains the various conditions employed with each ecosystem.

In universes B-3, E-2, C-1 and D-4, 5, and 6 no additional destruction was applied. The differences between them reflect the impact of the lesser or greater degree of built-in or inherent density-independent stress due to the hazards to movement. Universe B-3 was intended as a "control" for the others of this group, the aim being 100% utilisation of the food and thus the maximum mean standing crop of mites, the "equilibrium" density per whole-orange equivalent. During the later portion of this experiment (after some changes) approximately 96% utilisation was maintained and this was associated with a population of 2,600 mites, only 100

TABLE 1

Summary of equilibrium densities of *E. sexmaculatus* populations when *regulated* by competition for food under different density unrelated *conditioning* relations in controlled ecosystems.

	Only Built-In Hazards of Density-Independent Nature				*Additional Imposed Hazards of Density-Independent Nature*	
Equilibrium Estimates (per orange-equivalent basis)	B-3. 21 half-orange exposures, adjacent, remaining positions having rubber balls	E-2. 210 oranges 1/20 exposed, dispersed uniformly (no rubber balls)	C-1. 42 oranges 1/20 exposed, dispersed widely at random among rubber balls	D-4, D-5, D-6. 42 oranges 1/70 exposed, dispersed widely at random among rubber balls	I-7. 252 oranges 1/20 exposed, dispersed uniformly, 25% killed weekly (no rubber balls)	II-6. 252 oranges 1/20 exposed, dispersed uniformly, 50% killed weekly (no rubber balls)
Mean density	(*a*) 2,000 (*b*) 2,600	1,900	400	Indication less than 90	1,319	290
Food utilisation	(*a*) 74% (*b*) 96%	70%	15%	Indication less than 5%	49%	11%

less than the yardstick estimate of 2,700 at 100% utilisation. Prior to the change the mean density of this relatively unhazardous system was only 2,000, with 74% utilisation. In universe E-2 a maximum dispersion of the orange food was employed but no rubber balls were used; there was less hazard in this system than intended and the mean density was 1,900, with 70% utilisation. In universes C-1 and D-4, D-5, and D-6, on the other hand, the hazards proved greater than intended. It was expected that a more intermediate position would have resulted in universe C-1 and that the populations would not have died out in universes D-4, D-5 and D-6, as they did. Nevertheless, ecosystem C-1 demonstrates that with a fairly high intensity of action of mortality from losses in getting about in the system, the initial population stock can grow only to a moderately low level, 400, on the average, and although the population was buffeted about vicariously by chance factors of density-independent nature, competition for food regulated the population, although only 15% of the food was utilized.

Ecosystems I-7 and II-6 may be compared, and also with ecosystem E-2, which is comparable in all other respects and represents a level of *no* superimposed destruction. Thus, where no weekly destruction was applied competition for food regulated the population at 1,900 mites per whole orange equivalent and 70% utilisation. When a 25% weekly destruction was added the population mean was 1,319 mites and 49% utilisation. When a 50% weekly destruction was added, the mean density was 290 with only 11% utilisation of the food.

These results are comparable to early work on logistic growth of populations of water fleas and flour beetles under different temperature and humidity conditions, respectively (2), (6). The cessation of population growth in each of these systems illustrates the density-dependent *regulation* while a comparison of the levels at which the regulation occurs in different systems shows the equally important and inseparable concurrence, but distinct roles, of the two classes of factors, conditioning, legislative, or density-independent factors, and the density-dependent, regulating or density-governing processes.

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CONTRIBUTION TO THE BIOLOGY AND POPULATION DYNAMICS OF THE PINE SAWFLY *ACANTHOLYDA SERBICA* VASIĆ (HYMENOPTERA)

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This species was first described in 1962, attacking a thirty year old stand of *Pinus nigra* var. *austriaca* near Vrnjci Spa (Serbia). Vasic states that it was mixed with *A. erythrocephala* Chr. and *A. populi* L.

A. serbica is univoltine and prolongation of the diapause was once established in a small number. Adults appear in the last ten days of April and the average daily temperature for their appearance should be 10°C for 12-14 days. Flight is most intensive in the first ten days of May, the flight period lasting 26-35 days. Copulation takes 5-10 minutes and females copulate 2-3 times. Eggs are laid in rows on the underside of the previous year's needles, 26 being the greatest number laid by a female. Hatching of the larvae begins late in May or early June, and the larvae descend to the new sprouting bud where they spin a web in the form of a very thick nest full of excrement; each nest is occupied by several larvae. As they feed they move from the new to the previous year's needles. About 61·4% of webs are at the top, 20·8% in the middle and 17·8% on the branches nearest the ground. Larval life lasts 3-4 weeks and late in June or during July, larvae drop to the ground where they form hibernation cells. 84·5% of the eonymphs were found at a depth of 5 cm. and 15·5% at 10 cm. Larvae pupate in March and the pupal stage lasts 3-4 weeks.

Fig. 1 shows that the greatest number of eonymphs per square metre under trees was 2·4 in 1958. In 1960 it reached its minimum of 0·4 eonymphs.

Mortality due to parasites has not been noted but earwigs (*Forficula auricularia*) may be predatory. Even if this possibility is assumed, mortality would be only 19·8%. Mortality due to temperature during the first ten days of development of embryos is much greater. It can be seen from the figure that during the six years of study, this factor had its effects on the density because the movement of the curve of the average and minimum temperatures corresponds with the movement of population density curves. Consequently, this is one of the decisive factors governing population density.

Distribution of the population in 1958 was limited to the eastern half of the pine stand. During 1963, with increased density, it had spread throughout the whole stand.

It may be stated finally, that the biological distinctions between *A. serbica* and *A. erythrocephala* are quite clear and proves that the former is a separate species distributed over a considerable area of Serbia.

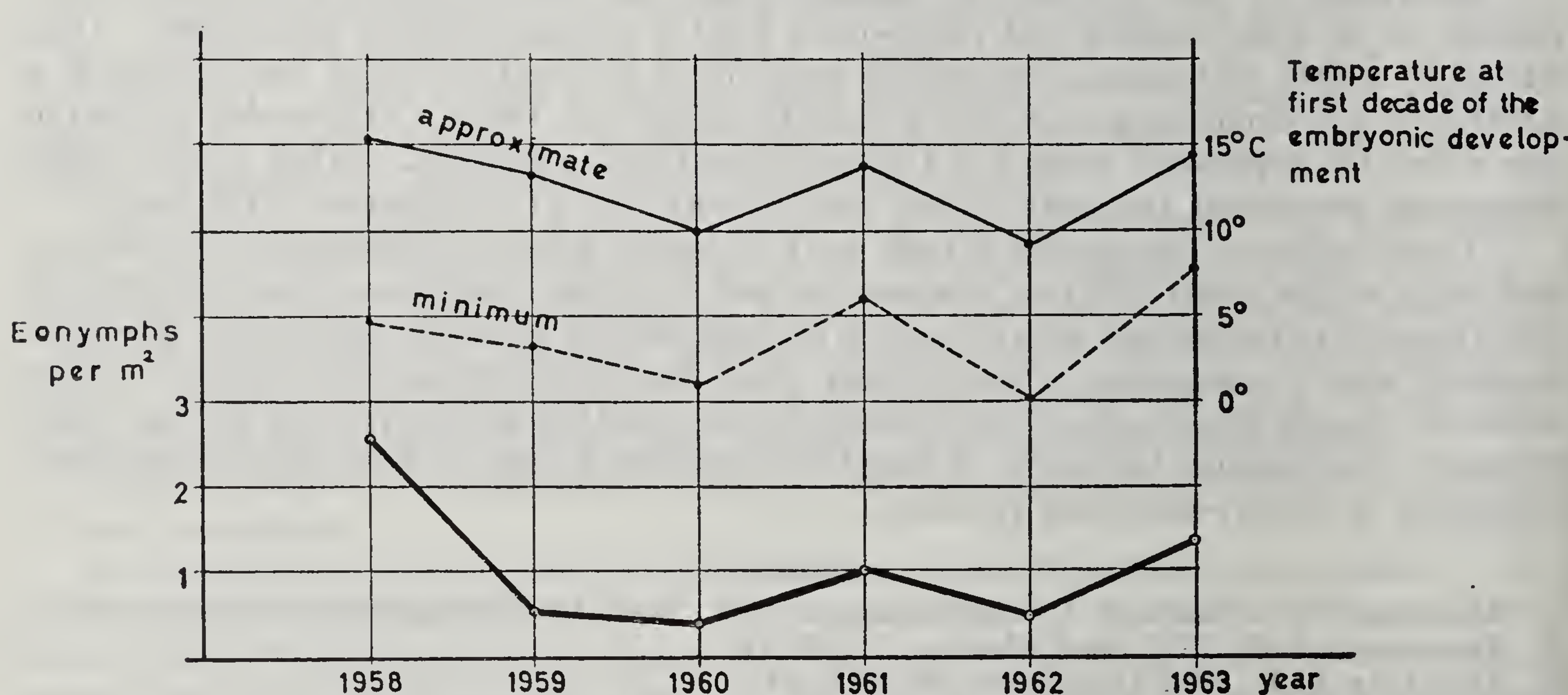

Fig. 1. The number of eonymphs of *A. serbica* per square metre of ground under trees during hibernation in the years 1958-63.

POPULATION DENSITY REGULATION OF *SMINTHURUS VIRIDIS* IN PASTURES WITH SPECIAL REFERENCE TO DENSITY-INDUCED CHANGES IN NUMBERS

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This paper summarises a nine-year study of the ecology of the lucerne flea, *Sminthurus viridis* (Collembola), in improved pastures in Western Australia.

Five processes contributing to population density regulation are described. There are (1) weather, which not only determines when the active stages may be present (from autumn through to spring) but influences numbers within the period of general favourability through its influence on soil surface moisture. (2) Soil type. *S. viridis* females require fine textured soils for effective oviposition; hence within any one season higher numbers are reached on soils with high silt and clay contents. (3) Botanical composition of the pasture. Broad-leaved plants are preferred and higher numbers are usually found where the proportion of broad-leaved plants is higher. (4) A predator. *Bdellodes lapidaria*, a bdellid mite introduced from Europe, is an efficient predator. If there are more than two of these mites per square foot early in the season (*i.e.*, in the autumn and early winter), *S. viridis* is unlikely to reach high numbers. There is about a two-month lag in the response of the mite to prey numbers so that an irregular predator-prey cycle is set up. (5) Density-induced cannibalism. Density-distribution maps show how in areas where initial densities are high, numbers tend to decrease whereas in areas where initial densities are low numbers tend to increase. Because of this the density-distribution of *S. viridis* in a pasture at the end of the season (September/October) may be the complete reverse of the distribution at the beginning of the season (April/May). Small samples of the environment (pasture plus soil) from areas containing large numbers of *S. viridis* are shown to be less favourable for new inhabitants than samples from low-density areas.

Young recently-hatched nymphs feed actively upon the dead bodies of recently dead nymphs and adults. In so doing they bring about their premature death so that in the field at high density few nymphs survive beyond the second instar. Sometimes a dramatic collapse of the population is brought about in this way. It is suspected that this process is associated in some way with the storage of excretory products in the fat-body. Individuals from high density areas have much greater amounts of uric acid in storage than those from low density areas. Possibly this may shorten life.

Experiments on individuals rather than populations are now planned in an effort to determine the source of the apparent "toxic material" obtained through this cannibalistic behaviour.

The processes regulating the numbers of *S. viridis* in pastures seem to fit in with the general theory of population density regulation as outlined by Nicholson (1954). The requisites for survival and multiplication are provided by the weather, soil and food. Within this framework *S. viridis* is competing for favourable space, *i.e.*, space containing these requisites but free from predators and dead bodies, both of which contribute to the premature death of this Collembolan. A knowledge of these latter processes is essential to a proper understanding of the changes in numbers observed in nature.

FACTORS INFLUENCING EGG SURVIVAL IN *SCOLYPOPA AUSTRALIS* WALKER (HOMOPTERA, RICANIIDAE) IN NEW ZEALAND

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Scolypopa australis is an Australian species which has been in New Zealand for at least 90 years. It occurs as far south as the Nelson district, being restricted to warmer areas over much of its range. The species attacks a great number of plants, for the most part feeding on their

more succulent portions. In 1945, following an outbreak of honey poisoning, *Scolypopa* was incriminated through its production of a poisonous honey-dew when feeding on *Coriaria arborea* Lindsay. A study of factors influencing egg survival was undertaken to prepare for possible parasite introductions from Australia.

Generally speaking, October, November and December are the months of nymphal emergence and development, and January, February, March and April those of adult activity and oviposition. The remainder of the year is spent in the egg which shows a typical diapause.

Eggs are implanted in the stems of a great variety of plants and in many situations. Late in the winter of 1962 oviposition materials were collected from more than 100 sites from throughout its range. Subsequent microscopic examinations involved more than 16,000 eggs.

Factors influencing egg survival may be divided into two categories—those of a physical and those of a biological nature.

The physical factors involve mainly the condition of host plant materials and their aspect. When green stems are used for oviposition, shrinking during subsequent drying out may damage eggs. Eggs laid in damp situations near the ground or where there is exposure to extremes of temperature show as much as 85% shrivelling. Northern averages of 30% fall to 3% at the southern edge of the range. Shallow implantation and the occasional use of hollow stems also account for small numbers of eggs.

The biological factors are more diverse. Stem-boring larvae of Lepidoptera and Coleoptera may destroy 60% of the eggs in some samples but the overall average is 5%. Gross implantation and cross puncturing may account for 50% of the eggs where high populations and small twigs are involved. Mite species, especially *Pyemotes* may destroy 12% of the eggs in some localities. The most important factor, however, is a hymenopterous egg parasite (*Centrodora* sp., Aphelinidae) which may show up to 87% parasitisation. This accounts for as much egg destruction as all other factors considered together. If the distributional range of *Scolypopa* is divided into six approximately North to South zones and the percentages of parasitisation calculated for each, these form a gradient with the figures 39%, 38%, 32%, 29%, 2%, nil, respectively.

If a division of the *Scolypopa* range into three North to South zones is made, and egg survival percentages are calculated, these show 27%, 45% and 93% respectively. Populations in the zones are not correspondingly great for a latitudinal range covering the southernmost extension of the species is involved. Northern populations are consistently large, whereas there appears to be a periodic abundance in southern areas dependent on conditions prevailing in successions of seasons.

QUALITATIVE CHANGES WITHIN FLUCTUATING POPULATIONS, INCLUDING GENETIC VARIABILITY

PREDICTING QUALITATIVE CHANGES IN INSECT POPULATIONS

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Genetic changes, according to some authorities (7, 11), play little part in regulating animal numbers. This paper presents an opposing view.

Fig. 1 (a, b) shows the seasonal rise and fall in numbers of two perfectly stationary populations: (*a*) where enemies are scarce, and climate, soil, food, cover, etc., are favourable for

survival and reproduction, and (*b*) where conditions are unfavourable. The consequent difference in average abundance *between* habitat types is one problem; another, more general problem, is to explain differences in numbers *within* habitat types (Fig. 1, c-e). Neither problem is likely to be solved except by comparative methods: in the first case by finding, through eliminative procedures, the relevant differences between habitat types; in the general case by comparing stationary or 'regulated' populations with expanding or 'unregulated' populations.

Fig. 1 (c, d, e) shows a population that increases at its maximum rate for one year, less rapidly for a second, and remains stationary for a third. For simplicity the weather and habitat are assumed to be the same each year; but with real populations this will not be so, and conclusions will be invalid in the absence of proper controls. The maximum possible rates of increase each year (c_1, c_2, c_3, which will normally differ) must therefore be found empirically, and compared with those actually observed in regulated populations. A further difficulty about real populations is that certain changes tend to occur at high but not at low densities—there is bound to be less food per individual as numbers rise, and disease and enemies are likely to be commoner. Perhaps such changes can prevent further increase in numbers; but evidence from mere correlations is useless since it does not distinguish between symptoms of regulation and the conditions necessary for its occurrence. This type of explanation, moreover, is inadequate where there are associated changes in quality (1, 3, 4, 5, 9, 10), and to at least some of these cases the following model, although inadequate itself, may be more relevant.

Two assumptions are made: (1) that all species have a dispersion mechanism, and (2) that

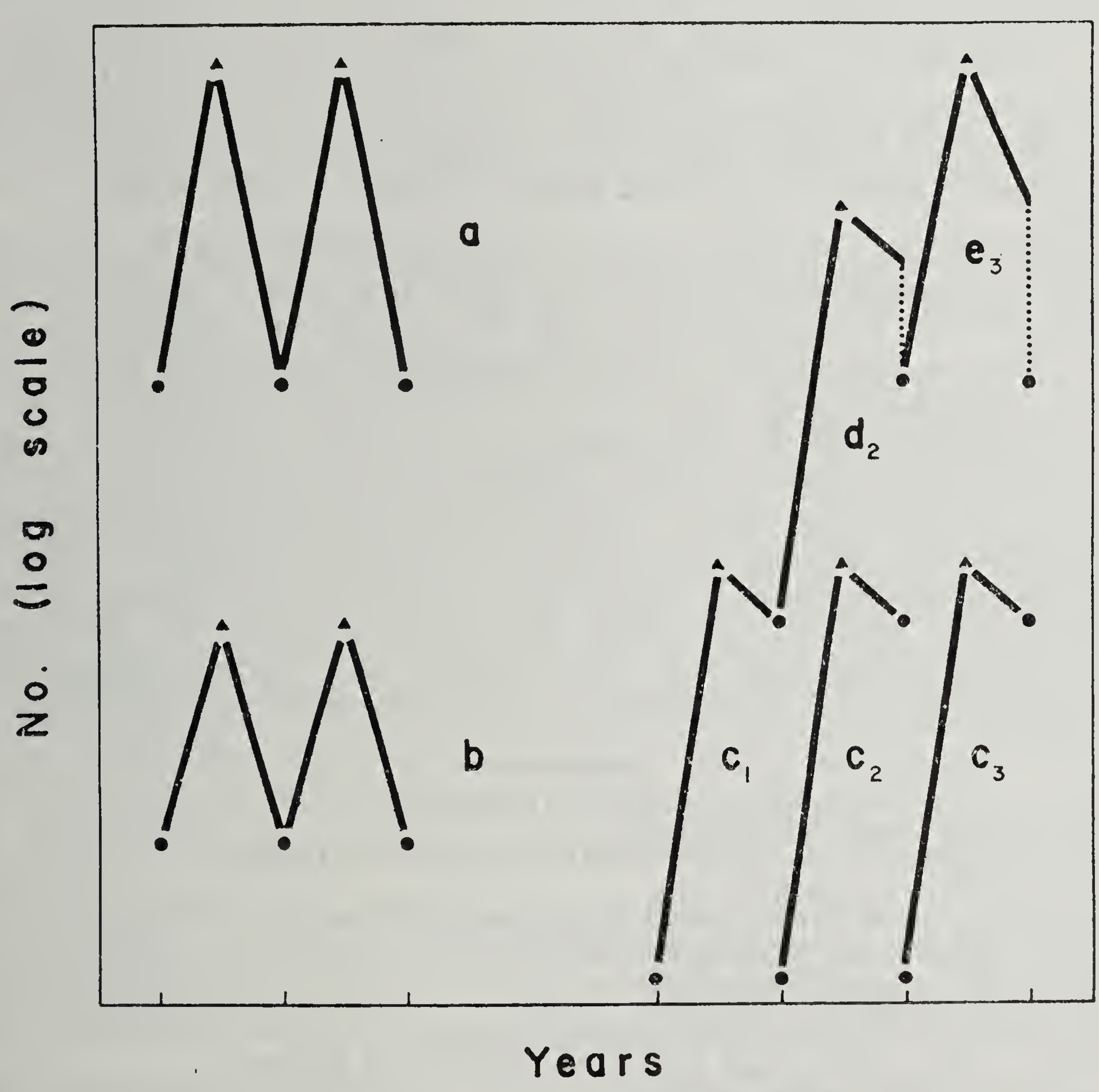

Fig. 1. Seasonal changes in abundance: in stationary populations in good and poor habitats (a, b); in expanding populations in good habitats (c_1, c_2, c_3), and in comparable populations (d_2, e_3) where surplus animals (dotted lines) are eliminated through some form of intraspecific behaviour.

selection for maximum fitness occurs at all population densities. Now in spacing themselves out, animals avoid some of their neighbours and threaten others, using a variety of means to do so (8). As numbers rise and fewer places are left, an animal's environment changes, and the selective advantage of "avoidance" seems likely to diminish in comparison with that of "threat" behaviour. We may therefore expect a change in the frequency of certain genotypes. And if selection, in the initial stages of expansion, favours the genotypes best fitted to purely local conditions, then at high densities there may well be relatively fewer animals possessing this type of fitness, and relatively more of those best fitted to survive and multiply under conditions associated with dispersion (6). In the denser populations the selective advantage will presumably be for genotypes that suffer least from intraspecific contacts, firstly by managing to remain in their preferred habitat at all, and secondly by having a worse effect on the physiology of their neighbours than *vice versa*.

If these inferences are correct losses in the non-breeding season in Fig. 1 may be partitioned as follows: in c_2 and d_2 losses due to local contingencies will be similar; but in d_2 there will now be additional losses through dispersion. Animals in the third year, having been selected for survival under conditions of mutual interference, will now differ from their controls. If this change in properties also reduces their fitness for the original conditions, the denser population (e_3) will have a lower birth-rate and higher death-rate than its control (c_3). In addition, since there is now a high proportion of animals selected for "threat", the direct losses through dispersion will also be more pronounced. In the poor habitats (Fig. 1b) events will be similar, but a smaller proportion of the population will be eliminated through dispersion.

This model, if true, accounts for the anomaly that the more favourable the habitat the higher the net annual mortality rate (slopes a > slopes b in Fig. 1). The model is not, however, known to be true, and although consistent with facts about mammal populations (2) has a number of wider but untested implications. And since these follow from perfectly general assumptions their truth or falsity can be judged from the results of predictions about appropriate populations of any species, including insects. Some of the more testable consequences are as follows:

(1) Apart from the predicted differences in behaviour between expanding and stationary (or declining) populations, there should be associated differences in physiology, which, as density increases, will increase the percentage of the population destroyed by weather. (2) Animals reared in isolated cultures should resemble those in expanding, newly introduced or severely exploited populations, rather than those in the majority of stationary populations. Colonies established from such stocks should tend to increase to abnormally high levels. (3) The genotypes that are most successful at high densities cannot be at an advantage all the time, because of seasonal and annual changes in the severity of local contingencies, and because favorable and unfavorable living space are generally interspersed. Some form of balanced behavioral polymorphism is therefore to be expected in most stationary populations.

According to this scheme, in contrast to that of Wynne-Edwards (12), numbers can be regulated by selection acting at the level of the individual, and qualitative changes associated with the process are a mixture of the phenotypic and genotypic effects of dispersion.

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POPULATION ECOLOGY AND GENETIC EVOLUTION

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The numbers and genetic make-up of all populations change through time. This important evidence has not been given sufficient consideration in the study of the ecology of populations. The attention of this research focuses on the role natural selection and genetic change play in both natural population regulation and the outcome of interspecific competition.

Through the action of the genetic feed-back mechanism (Amer. Naturalist, 1961) parasites, predators, herbivores, and competitors can be regulated and gradually evolve toward homeostasis with their community associates. Densities of the eating animals and interspecific competitors exert important selective pressures on their interacting hosts or competitor populations; selection influences genetic make-up in turn, the resulting genetic changes alter the characteristics of the eating and competing species. In laboratory research (Proc. XVI Int. Congr. Zool., 1963) designed to determine if the numbers of a wasp-parasite (*Nasonia vitripennis*) population could be regulated by genetic changes in the housefly-host (*Musca domestica*) population, a constant number of hosts were supplied daily to the parasite population. After nearly three years of interaction, the host has evolved a degree of resistance to the parasite, while the parasite has evolved an avirulence. The reproductive capacity of the parasite on its host has declined about 72% and this decrease in biotic potential resulted in a 50% decline in the average density of the parasite population. The amplitude of the fluctuations in this parasite-host system has gradually decreased.

The action of the genetic feed-back mechanism in controlling the numbers of a wasp parasite on its housefly host was further studied (Amer. Naturalist, 1963) using a special multicell population cage in which the parasite and host can interact without external manipulation. The amplitude of the population fluctuations in the experimental parasite-host system which evolved a degree of ecological homeostasis was less than that exhibited by the control or wild parasite-host system. Evidence suggests that environmental resources were used more efficiently in the experimental parasite-host system.

Interspecific competitors may change genetically with the result that competing species can coexist in the same ecosystem (Proc. XI Int. Congr. Genetics, 1964). As a competing species becomes the dominant species, it is at an evolutionary disadvantage because intraspecific competition is the main selective force acting on it. The sparse species, however, because it is under selective pressure brought by interspecific competition has an evolutionary advantage. Given sufficient time a genetic adjustment between the competing species should result.

To test this theory two competitors, the housefly and blowfly (*Phaenicia sericata*) were released in opposite corners of a multicelled cage (Amer. Naturalist, 1965). At first the housefly population suppressed the blowfly population, but in time the blowfly increased, became the dominant species and eventually caused the extinction of the housefly. A check of the blowfly population when it started its comeback showed that it had evolved into a more effective competitor than the housefly. To see if these two species can evolve, coexist and occupy the same niche, a multicell cage with increased space-time structure is now under investigation.

Thus, the genetic feed-back mechanism by regulating animal numbers helps to maintain population stability. This same mechanism may bring about the coexistence of competing species and increase species diversity. Both population stability and species diversity are important characteristics of natural communities as they evolve toward ecological homeostasis.

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VARIATION IN SIZE IN THE WORKER CASTE OF *BOMBUS FERVIDUS* (FAB.)*

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Considerable variation exists in the sizes of worker bees in a bumble bee colony. The differences can be expressed by measurement of weight, wing length, or length of the radial cell of the forewing. The latter method was used in connection with tongue-length research (4), and proposed as a convenient method of size determination.

Little is known about the mean sizes of worker bees within and between colonies. This information should be useful to help elucidate certain problems of bumble bee biology, such as colony vigor, caste determination, and number of bees produced.

Samples of worker bees were obtained from 37 colonies of *Bombus fervidus* during 1960-63. The radial cells were measured with a 50-unit micrometer scale inserted in the ocular of a binocular microscope. The scale was calibrated so that 10 units equalled 1 mm. All measurement data in this report are given in the original units of 0·1 mm.

The bumble bee colonies were collected from natural locations at various stages of development and transferred to wooden box domiciles for eventual production of males and queens. Two colonies were started in the laboratory and then allowed to develop in the field. As these colonies were used for various experiments, some were terminated before the maximum production of workers or the appearance of sexual castes. Twenty-five colonies completed the normal cycle of development to the extent of producing males and queens. Whenever possible a comb analysis was made to obtain an estimate of the total number of cells of the castes in a colony.

The mean size of the radial cell in the total sample of 1,866 worker bees from the 37 colonies was 32·83. The means of colonies ranged from 28·73 to 36·46. An analysis of variance of these data showed that the means between colonies differed significantly at the ·01 level. The 1962 and 1963 colonies had means of 32·71 and 33·28, respectively, and the difference was significant at the ·01 level. Within each of these years the differences of means between colonies were highly significant also.

Table 1

Caste production and radial cell length of worker bees in ten colonies of *B. fervidus*

Colony Number	*Total Production*			*Workers Measured*	*Mean*	*Standard Deviation*	*Range*
	Workers	*Males*	*Queens*				
63-59	237	41	11	73	30·86	4·25	22-40
63-48	168	4	44	136	31·91	3·89	20-43
62-15	198	48	21	105	32·13	2·92	24-39
63-55	192	62	11	33	32·36	3·44	24-39
62-33	190	61	53	85	32·52	3·69	22-39
63-57	175	49	23	39	33·0	4·32	26-42
62-17	206	25	34	84	33·04	3·91	20-39
63-54	241	27	32	68	33·72	2·56	26-41
63-5	215	17	78	128	35·23	3·42	23-41
63-47	175	47	67	119	36·22	2·67	27-40

Data on the total production of the three castes of bees, and on the means and standard deviations of the worker samples taken from ten of the largest colonies are given in Table I. The analysis of variance showed that the differences of means between the colonies were significant at the ·01 level. There appeared to be no correlation between the mean size of the workers in a colony and the total number of bees that were produced.

In four colonies (63-44, 34, 45 and 43), samples were taken on those bees produced early in the development of the colony. The samples collectively represented 56 per cent of the first workers produced. The means were 31·07, 31·87, 32·53 and 33·29 respectively. The differences between the means were not significant.

Also, in four other colonies the measurements were obtained on workers sampled at both

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early and late periods. No significant differences were found between the means of early and late bees, except in colony 63-48, where the difference was significant at the ·05 level. In this nest the late-produced bees were smaller than the early-produced bees.

A histogram showing the distribution of the 1,866 measurements approached a normal distribution curve but there was some indication of bimodality. The histograms of the colonies themselves showed considerable variability, and most were either skewed or bimodal.

Discussion. It is generally accepted that the variable sizes of bumble bees are directly associated with the unequal nutrition of larvae. Clusters of bumble bee brood are developed progressively during the colonial cycle, and the total amount of food in the various clusters may differ. Also, within any particular brood cluster the food available to a larva differs according to its central or peripheral position in the cluster, or its random feeding by the nurse bees. Several factors that are responsible for the marked variation in size between bees of one egg cluster were discussed by Cumber (3).

The significant differences that existed in the mean sizes of worker bees measured in this study probably can be explained on the basis of different amounts of food in various colonies, providing that unbiased samples were represented. Biased samples would be caused by measuring too few bees in relation to the total workers, or the heavy loss of foraging bees at the time colonies were taken from the field. It is well-known that guard and nurse bees in a colony are smaller than foraging bees. This division of labor was shown for *B. agrorum* (Fab.) (2, 3 and 6) and for *B. medius* Cress (5). However it is believed that an adequate sample of the larger, foraging-type bees was obtained in most of the 1962 and 1963 colonies of *B. fervidus*, as the samples usually were obtained from domiciled colonies brought back to the laboratory at night after most bees had returned from the field. The colonies studied in 1960 and 1961 perhaps had inadequate samples, as the means all were below average.

Although differences in means of colonies is probably caused by differences in food supply, it is not clear whether the differences in food are the result of intrinsic or extrinsic factors. Brian (1) explained the difference in average size of workers in two nests of *B. agrorum* between two years on the basis of weather factors, with a lower average in the bad year. As there were highly significant differences in the means within each of the two years with a long series of nests (1962 and 1963), differences in weather factors would not satisfactorily explain the variation found in the above colonies.

The fact that the differences in means of early-produced bees was not significant in 4 colonies is suggestive that certain unknown differences in colony biology during later periods of the colonial cycle may be responsible for the trends to larger or smaller bees.

The lack of significant differences in means between early-produced and late-produced bees in 4 other colonies is in agreement with comparable data on *B. agrorum*. Cumber (3) and Brian (1) showed that the seasonal picture is not one of gradual increase in the average size of workers. The preponderance of workers of smaller size as the season progresses was explained by Cumber on the basis of a precarious food balance in the colony during the expansion of the colony, which tends to increase the number of smaller workers.

No association was found between the mean size of workers and the total number of workers produced (as determined by cell counts). But it was interesting to find that four of five colonies with worker populations of 50 or less had lower than average means, whereas, four of five colonies with worker populations of 200 or more had higher than average means.

No consistent interrelations were found between the mean size of workers and the number of males and queens. However, the data indicated that large colonies with higher than average means produced more queens than large colonies with lower than average means.

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INDIVIDUAL VARIATION IN OVARY DEVELOPMENT AND IN REPRODUCTIVE BEHAVIOUR OF *OSCINELLA FRIT* L. (DIPTERA)

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The variation in oviposition of individual adult females of *Oscinella frit* on young oat plants was determined at 20°C constant temperature. The preoviposition period of 40/60 females varied from 3 to 6 days, and in the remainder from 7 to 45 days. Eggs were laid in batches, initially at intervals of 1 to 3 days, each batch representing a set of ovariole cycles. Females with short preoviposition periods tended to have shorter interoviposition periods and higher fecundities.

Newly emerged virgin females, caged with young oat plants in the absence of males did not oviposit for at least two weeks, but maturation of the ovaries proceeded, each cycle of eggs being retained. The eggs produced in a set period of 12 days were determined by dissection and the effects of males and oviposition stimuli thus eliminated. The number of fully developed eggs divided by the number of ovarioles, for each female examined, gives the number of cycles which occurred in each ovariole. In 450 flies thus treated, 2% contained no eggs, 35% contained eggs equivalent to 1 ovariole cycle, 48% 2 cycles, 14% 3 cycles, and 1% 4 cycles. These results confirm the individual variation in preoviposition and interoviposition periods demonstrated with females reproducing normally.

550 females were treated as before but without oat plants. 44% developed no eggs, 55% 1 cycle, 1% 2 cycles and 1 individual 3 cycles.

The host plant, therefore, stimulates ovary maturation but response varies with the individual.

The mean number of ovariole cycles for batches of 100 females caged with a series of host and non-host Graminae for 12 days demonstrated that different plant species varied in their capacity to stimulate ovary maturation. Oats exceeded all with a mean of 1·5 cycles, most of the other recorded larval host Gramineae induced about 1·1, and the non-host *Dactylis* induced 0·7 compared with 0·4 in the absence of any plant.

The mean pre-oviposition period of flies ovipositing on the hosts *Arrhenatherum elatius* and *Lolium perenne* was about 6 days, compared with 4½ days for oats. On *Dactylis glomerata* no fly took less than 8 days and about one-third of the individuals had not oviposited after 30 days.

It is concluded that the length of the preoviposition period and the rate of egg production depend on the amount of stimulation required by the individual for ovary maturation, which in turn depends on the stimulating powers of different host species.

The minimum preoviposition period was increased by about 3 days for small flies (produced by crowding the larvae) compared with larger flies; otherwise the variation appears to be primarily genotypic.

The adult frit fly must be dispersive and this genotypic variation would ensure a range of forms, those with short preoviposition periods undergoing only limited migration, and at the other extreme, forms able to undergo long distance migration before commencing oviposition. The proportion of these forms would depend on the host species available.

THE BIOLOGY OF *OSCINELLA FRIT* L. (DIPTERA: CHLOROPIDAE) IN N.E. ENGLAND

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In N.E. England the synchronisation in phenology between *O. frit* and the oat crop breaks down. This is attributed in part to low spring and summer temperatures, in part to changing host preferences during the season and in part to protracted development at higher temperatures of the flies themselves.

Continuous trap and sweep records of the abundance of *O. frit* in oats in Northumberland

(1956-1962) revealed two maxima per annum. As in the south of England the first peak constituted overwintered individuals, the second, individuals which had emerged from tillers in the crop. The first was usually the most pronounced and the second occurred between mid-July and early August according to weather. Even on late sown plots there was little evidence of second and third peaks which greatly exceeded the first in magnitude as described by Jepson and Southwood (1) for Berkshire.

Particularly in commercial crops there was very little oviposition on the developing panicles and low levels of grain attack were attributable to oviposition on the unopened panicle sheaths, the spikelets containing pupae or fully grown larvae at panicle burst. Oviposition on the spikelets themselves occurred only when the weather in late May and June was unusually warm (air temperatures above 70°F.) and development of the tiller generation was accelerated; in cold springs the flies did not emerge from the tillers until the spikelets had passed the most susceptible stage of development. In such years no eggs at all were laid either on young oat plants or on newly emerged panicles after mid-July, even though both were supplied by successional sowings and gravid female flies were in good supply.

Both phenological and host preference effects were apparently involved, as by the autumn the running total day degrees above 42°F are only two thirds of the comparable total for the south of England and young oat plants are preferred to wheat for oviposition in spring and autumn but not in summer when the two hosts are equally attractive.

The imagines collected in Northumberland were almost totally black and resembled the *O. frit* type A or B described by Choyce (2). Type C flies with light tibiae such as comprise the bulk of the populations further south were scarce at all times. A population of northern flies, reared in the laboratory at high temperature (70°-80°F) resembled type C individuals after seven consecutive generations. The mean duration of development of these flies, in terms of the day-degrees required to complete it, also decreased from 968 to 468 suggesting that the population initially contained long development forms. A similar effect was recorded by van Emden *et al* (3) in the field and it is surmised that such individuals possess a selective advantage by continuing development at low temperatures at which type C individuals are quiescent. Their preponderance in northern Britain suggests they are a further extension, specifically adapted to cool maritime climates with short summers, of the *O. frit-O. pusilla* series described by Karpova (4).

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LA RESISTANCE AU JEUNE DES IMAGOS ISOLES ET GROUPES CHEZ *LOCUSTA MIGRATORIA MIGRATORIOIDES* (R. ET F.)

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Phase solitaire

Il s'est averé indispensable d'étudier le déterminisme du polymorphisme chromatique chez les solitaires avant d'aborder le problème de leur résistance à la dessiccation et à l'humidité elevée; en effet, des expériences préliminaires ont revelé que les différences de coloration chez les animaux elevés en isolement se soldent par des différences de vitalité.

Deux facteurs interviennent dans le déterminisme du polymorphisme chromatique.

C'est le degré hygrométrique qui induit ou interdit le verdissement des larves maintenues en isolement. L'elevage à 100% d'humidité relative entraine le verdissement de tous les animaux dès le 2ème âge. Aucun individu ne verdit à moins de 30% d'humidité relative. Les isolés verts sont *minoritaires* jusqu'à 50% (verdissement au 5ème âge) et *majoritaires* à partir de 60% d'humidité relative (verdissement aux 3ème et 4ème âges). La coloration verte de la vegetation n'a pas d'influence sur le tegument. Le virage au vert se produit dans les 24 h. après la mue aux 2ème et 3ème âges, les 48 h. après la mue aux 4ème et 5ème âges, 1 à 4 jours

après la mue chez l'imago, *la cuticule non encore durcie.* Il n'a plus lieu à partir du 5ème jour qui suit la mue imaginale. Les animaux verts ne revirent au brun que lors d'une chute importante de l'humidité ambiante. Ce retour à la couleur primitive est *continu* et *progressif*; il exige deux intermues lors du retour au climat sec de larves vertes du 2ème âge, est très partiel et tardif lors de ce retour chez les larves du 5ème âge, ne se fait plus jamais complètement chez l'imago.

La couleur de fond du biotope agit sur les isoles qui n'ont pas verdi. Le maintien sur fond jaune, gris ou noir des imagos bruns *majoritaires* se traduit dans tous les cas par un changement rapide de la couleur tegumentaire. Les individus n'ayant pas verdi malgré l'humidité relative elevée (imagos bruns *minoritaires*) ne réagissent que dans deux cas sur trois; il en va de même pour les larves de coloration brune. L'adaptation chromatique se fait progressivement, en dix jours environ, *après le durcissement de la cuticule.* La livrée noire n'est pas définitive et peut disparaitre lorsque l'animal est transferé dans une cage à parois blanches. La couleur de fond n'agit pas sur les animaux aveuglés.

La livrée des animaux s'harmonise donc dans la majorité des cas avec la teinte de fond du biotope habituel. L'humidité elevée induit à la fois la coloration verte des animaux et la teinte verte uniforme de la vegetation (adaptation chromatique *indirecte*). L'aridité interdit le verdissement à la fois des animaux et du biotope: les isolés restés bruns s'adaptent *directement* à la gamme de teintes de la vegetation dessechée ou brulée. Les *minoritaires* bruns représentent la seule exception.

A la différence de coloration des imagos bruns et verts correspond une différence importante dans la résistance au jeûne suivant le degré hygrométrique. C'est le solitaire vert qui survit le plus longtemps dans une ambiance humide, le solitaire brun qui résiste le mieux à la dessiccation. Le délai de survie moyen des animaux *majoritaires* à 95% d'humidité relative est de 195 h. pour les solitaires verts et de 150 h. pour les solitaires bruns; à 30% d'humidité, il est de 143 h. et de 184 h. respectivement. L'écart entre les valeurs obtenues aux deux niveaux hygrométriques est réduit lorsque ces mêmes expériences portent sur des isolés de filiation groupée.

Ces différences de résistance persistent encore lorsque l'on établit des comparaisons entre animaux *majoritaires* et *minoritaires.* Les isolés verts et bruns existent en proportions variables dans toute population naturelle de solitaires; c'est ce qui permet d'apprécier à sa juste valeur l'importance que présentent ces différences de résistance entre *majoritaires* et *minoritaires.* La *stabilité* des conditions écologiques favorise la survie des animaux *majoritaires*; les *minoritaires* paraissent au contraire préparés à assurer la persistance de la population en cas de *changement* des conditions hygrométriques.

Phase gregaire

A lui seul, le *groupement* au cours du développement postembryonnaire ne suffit pas à déterminer une résistance plus elevée dans des conditions d'existence moins favorables. D'autres facteurs interviennent, et doivent être pris en considération.

L'*état hygrométrique* du milieu d'elevage retentit lui aussi sur les résultats; le fait d'avoir elevé les groupés, non pas dans une ambiance sèche mais à forte humidité, augmente quelque peu leur résistance à l'humidité.

A coté du facteur hygrométrique, la *filiation* retentit sur la résistance au jeûne des imagos groupés; celle-ci est réduite chez les individus groupés de filiation isolée.

Mais il ne s'agit là que de différences de degré, de différences *quantitatives. C'est l'action de la photopériode qui conditionne la grande résistance, soit en milieu humide, soit en milieu sec* (*différence qualitative*). Le maintien des élevages groupés à une période d'éclairement *courte*, correspondant à la durée du jour *Soudannais* (latitude 15°) au moment du solstice d'hiver, se traduit par une augmentation moyenne de la survie dans une ambiance *sèche*; par contre, une photopériode *longue* (durée du jour au moment du solstice d'été) préadapte les animaux à une ambiance fortement *humide.* Ces différences de vitalité sont à mettre en parallèle avec les conditions climatiques dans lesquelles vivent ces Acridiens: au jour court (solstice d'hiver) correspond la saison sèche, au jour long (solstice d'été) la saison des pluies. En été, les grégaires mis à jeûn survivent plus longtemps à l'humidité que ne le font les solitaires verts; en hiver, leur résistance à la dessiccation est augmentée par rapport à celle des solitaires bruns. C'est donc au photopériodisme qu'est dévolu le rôle d'*indicateur*, du moins chez les *Locusta* grégaires: il ajuste la physiologie de ces derniers au cycle saisonnier.

INDIVIDUAL DIFFERENCES IN *MALACOSOMA NEUSTRIA* (L.)

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Before discussing the possible influence of individual differences on insect population dynamics, we should like to present briefly some observations on *Malacosoma neustria* (L.). Following the example of Wellington (4, 5) in Canada, who worked with Nearctic tent caterpillars, we have studied possible differences between individual larvae and adults (1, 3).

First instar larvae were separated according to their behaviour in a light gradient. Starting 93 cm distant from the light source (60 watt bulb) freshly hatched and non-fed larvae behaved quite differently: some crawled more or less straight to the light, independently of other larvae (type I). Most of the larvae did not move at all or not in a directed way and did not approach the light (type II). Both types were separated. The behaviour of the individuals remained very constant; it was, therefore, considered not to be the result of a changing mood or of short-time active and resting periods. In 10 minutes, at least 91% of the larvae showed clearly whether they belonged to type I or type II. The numerical relation between both was between 1 : 3 and 1 : 4 (type I : type II). Offspring of selected individuals showed increased differences in the first generation, and still statistically significant differences in the second generation in spite of a general shift towards type II in this year. The frequency relation between both types was unchanged if hatching was stimulated earlier and diapause shortened by temperature manipulation. Those larvae that left the egg masses first and crawled away after hatching were not predominantly type-I larvae. Sex ratio was also equal in both types.

With adults, differentiation between both types was not so easy. Adult males, however, from type-I larvae showed clearly a higher flight activity in captivity which could be measured by the degree of wear of their wings. The same tendency was present with female adults, but not so clearly expressed. So far, observations corresponded to those made by Wellington on *Malacosoma pluviale* (Dyar). But the subtypes (II, a, b, c) discussed by this author could not be detected in *M. neustria.* Further, the construction of the tent, so useful as indicator of the type composition of a colony, was greatly different with *M. neustria.* There was no tent as shelter for larvae at night or during bad weather. The silk produced by the Palaearctic species was mostly spread on one branch and served apparently only as a support during moulting. Thus, with the decreasing importance of the silk shelter for the survival of the colony, its value as indicator of colony composition disappears. In *Malacosoma neustria*, individual differences were studied of: (*a*) the tolerance of extreme temperatures; (*b*) tolerance of starvation; (*c*) reaction against parasitization; (*d*) susceptibility against infection by pathogens.

(*a*) Second instar larvae of both types were reared to pupation at 15, 21 and 28°C. At 21°C the developmental period was approximately equal for both types. At 15°C neither type reached the pupal stage. Whereas type-II larvae became 3rd instar larvae after 19 days and survived up to 73 days, type-I larvae died all before they reached the 3rd instar. At 28°C the tolerance was reversed: type-I larvae developed without losses and became pupae after 28 or 29 days; type-II larvae died after 6 to 9 days without reaching the 3rd instar.

The simultaneous occurrence of two *larval types of different temperature tolerance* might be of value for the survival of the species.

(*b*) *Tolerance of starvation* was tested with freshly hatched larvae. The LT_{50} was 2·5 days shorter with type-II larvae as compared with type-I, at 11°C. Type-I larvae were more active when searching for food and thus more successful in locating it after a period of starvation.

(*c*) Parasitisation by the tachinid fly *Mericia ampelus* Wlk. was used to give information on *differences* in *host susceptibility* and power of *incapsulation.* The tachinid used produces living larvae. These could be applied ventrally to third instar larvae. The parasite then entered the host usually after 10 to 200 seconds. The caterpillars were fixed at regular intervals and the following summarizes the results of histological studies: There was no difference in successful establishment of parasite larvae. Both types of host larvae harboured about the same (high) percentage of developing tachinid larvae. The reaction of host larvae, however, differed significantly. Type-I larvae showed, on an average, a thicker layer of hemocytes than type-II larvae. Evaluating these observations causes some difficulty owing to the simultaneous

occurrence of a nuclear polyhedral disease. As type-II larvae generally are more heavily affected by this disease, it might be that reduced hemocyte layers in this type were directly influenced by the virus diseases and only indirectly by the type of the larvae (2).

(*d*) The incidence of disease was more frequent in type-II larvae during all experiments. The occurrence of a nuclear virus disease in the total stock after two years of rearing interfered with most experiments. A deposit of approx. 2000 spores plus crystals per cm^2 of *Bacillus thuringiensis* was applied to the leaf surface by spraying. Freshly moulted 3rd instar larvae of both types were fed with these leaves for 48 hours. Measuring their feeding activity revealed no differences. The mortality, however, differed greatly. It reached 28% with type-I and 71% with type-II larvae (42 specimens each). A repetition yielded 33% for type-I and 74% for type II (70 specimens each). Thus, the active and more vigorous type-I larvae are more tolerant of *Bac. thuringiensis* spores and crystals. Application of insufficient dosages in the field may remove sluggish types only and select type-I larvae for survival, a result certainly not favourable to the farmer.

The occurrence of polymorphism "*per se*", as described above, lends support to the view that this phenomenon influences population dynamics.

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METHODS OF OBTAINING AND ANALYSING DATA ON INSECT POPULATIONS

CAPACITY FOR INCREASE OF THE GARDEN CHAFER, *PHYLLOPERTHA HORTICOLA* (L.) (COLEOPTERA)

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A new term, Capacity for Increase (r_c), is proposed. The term is given by the equation

$$r_c = \frac{\log_e R_o}{T_c}$$

where R_o is the net reproductive rate, and T_c is the length of a generation (calculated as the mean age of mother at birth of offspring). The term has long been regarded simply as an approximation for r_m, the innate capacity for increase in numbers, but it is suggested that the term also has biological meaning in its own right.

Calculation of r_c is illustrated using a life table and fecundity schedule for the garden chafer, a grassland beetle with an annual life cycle. There is no overlap of generations, hence r_c accurately describes the garden chafer's power to multiply.

It is further shown that continuous breeding gives a boost to reproductive power that can be regarded as an extra bit added to r_c (the size of the bit depending on R_o and on the fraction of life taken up by breeding). Yet r_c still has meaning since (*a*) the number of individuals in a generation is exactly R_o times the number in the preceding generation and (*b*) the mea birth dates of succeeding generations are exactly T_c time units apart.

Full treatment of this subject is given in Laughlin (1965).

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THE NEGATIVE BINOMIAL DISTRIBUTION AND THE SAMPLING OF INSECT POPULATIONS

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In 737 samples of 500 g of grain taken in series of 8-12 on 6 dates at 3 depths in 4 rooms, the distribution of *Calandra granaria* agreed with the negative binomial with a common k (0·2). The variance was not stabilised by any of the common transformations, including $k^{\frac{1}{2}}\sinh^{-1}(x/k)^{\frac{1}{2}}$. This is due to k and the mean being so small $(0 \leqslant m \leqslant 3)$.

One or both of these parameters may be increased by either increasing the sample size or pooling independent samples. This was tested on the distribution of *Culicoides* larvae in 16 square grids of 4×4 square samples (1). From these observations two sequences of 5 series of 16 samples were formed, the samples being sums of 1, 2, 4, 8, or 16 original samples. In one sequence adjacent samples were pooled, in the other sequence the samples to be pooled were randomly selected out of all 256 original samples. The values of k assumed in these 2×5 series were:

number of samples added	1	2	4	8	16
adjacent samples	0·21	0·08	0·11	0·22	0·34
random samples	0·20	0·39	0·82	1·27	5·79

This shows that while k is hardly affected by the sample size (pooling of adjacent samples) it is directly proportional to the number of random samples pooled.

A compatible observation was made comparing the above grain samples of 0·5 kg with a parallel series of 29 samples of one ton. These were composed of 20 sub-samples from different sections and/or depths of the grain bulk, and each sub-sample was composed of 2 sub-sub-samples (of 25 kg) from different places within the same section and depth. As the twin sub-sub-samples are not entirely independent the one-ton-samples should show a value of k 20-40 times that of single samples. In fact it was 30 times that of the 0.5 kg samples (6/0.2).

Mathematically the question may be illustrated by the equation:

$$s^2 = m + m^2/k \qquad (1^*)$$

If p independent samples are pooled m and s^2 will both increase p times, and if the expectation of m/k is constant throughout the area of observation the resulting distribution is again negative binominal:

$$ps^2 = pm + (pm)^2/x$$

which together with (1*) gives

$$x = pk$$

Thus the parameter k has also increased p times.

If, alternatively, the sample size is increased p times, the increase of s^2 will depend on the gradient of density, which is usually small owing to aggregation. If the gradient approaches zero and the sample size is increased p times, the variance will increase p^2 times:

$$p^2s^2 = pm + (pm)^2/x$$

which together with (1*) gives

$$x = k/(1 + (1 - 1/p)(k/m)) < k.$$

Thus k may even decrease with increasing sample size.

Conclusion: If m and k of the negative binomial distribution are too small for transformations to stabilise the variance, summation of random samples is advisable. Sample size usually affects mean only.

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A NATURAL LAW FOR THE SPATIAL DISPOSITION OF INSECTS

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Biologists are interested both practically and theoretically in the spatial disposition of organisms. Practically, the problem arises in census surveys of numbers per unit area. Artificial populations, such as crops, usually have plants uniformly arranged so that the number in each unit area is the same. In natural populations this is rare. Numbers differ from unit to unit and frequency distributions of numbers of organisms per unit area, in samples from different populations of the same species, are often of different structure. For example, different populations of larvae of *Pyrausta nubilalis* (Hubner), the European Corn Borer (fig. 1), are described efficiently by Neyman's Type A, B or C distributions, by Polya's Type 1 or 2, by the negative binomial, by the Poisson binomial, by several of these or by none (1, 4). Thus several different transformations may be necessary for the same species, making analysis difficult. The theoretical approach to spatial disposition also often uses frequency distributions. For example, Neyman's, Polya's and Thomas's distributions are all derived from hypotheses about the factors concerned in spatial disposition and the exponent k in the negative binomial expansion is a theoretical index of aggregation. However, neither these distributions nor the index k are universally applicable.

Skellam (5) concluded that satisfactory description of frequency distributions is usually possible on a wide range of alternative hypotheses and both Bliss (2) and Waters (8) suggested that the negative binomial is particularly useful because it can arise from at least 5 different models. Extending this line of reasoning it appears that a wider approach than frequency distributions may be valuable. Current statistical practice tends to regard spatial disposition as static, at least during the course of the experiment, but, population density is like the surface of the sea, always changing in space and time, and spatial disposition is like the pattern of the waves. If this pattern is measured by an isolated, instantaneous sample taken at a homogenous small area selected from a more heterogeneous background, it is unlikely to show the highly specific character of the whole surface. To see this overall pattern, it is necessary to relinquish some of the detail, see all the samples together, and seek the continuity connecting them.

In a sample consisting of a large batch of units taken simultaneously, the mean is a fixed value, defined within limits of error, and the variance is equally well defined. If, instead of collecting units in batches, however, we collect them in pairs scattered over space and time, and consider the means and the differences between pairs, it is more evident that the mean and the difference, which is a measure of variance, are continuous functions one of the other. It is in this functional relationship that the general description of spatial disposition lies. Variance (S^2) is related to the mean population density (m) by a Power Law: $S^2 = a\, m^{b}$, which is most conveniently illustrated, and fitted, as a regression equation in logarithms:

$$\log (S^2) = \log a + b \log m$$

where $\log a$ and b are intercept and regression coefficient respectively. 24 census surveys of organisms from all sections of plant and animal kingdoms have already been shown to obey this natural law (6).

The index b ranges widely in different organisms but remains constant for the same organism in the same environment even when sampled by different methods. Different sampling methods and perhaps also population growth rate, change a, whilst it seems possible that b may reflect the behavioural interaction between organism and environment. What other factors are involved remains to be seen, but changes in the spatial pattern resulting from changes in population density are evidently restricted, for any given species, to a narrow range. This could not be anticipated from analysis of frequency distributions, which differ as much between different population densities as between different species.

From the specific relationship between sample mean and variance, another species characteristic follows. Taylor (7) showed that the relationship $S^2 = a\, m^{b}$ gives rise to a system of transformations derived from the transformation function:

$$\varphi\,(m) = Q\int m^{-b/2} \mathrm{d}\, m.$$

From this, the quantity to be analysed (z) is transformed from any original count (x) by

the expression: $z = x^{1-\frac{1}{2}b}$.

Values for $(1-\frac{1}{2}b) = 0{\cdot}2$, $0{\cdot}4$, $0{\cdot}6$, $0{\cdot}8$ and equivalent values for $-0{\cdot}2$, $-0{\cdot}4$, $-0{\cdot}6$, $-0{\cdot}8$ are given by Healy and Taylor (3). Tables for $(1-\frac{1}{2}b) = 0$, $0{\cdot}5$, $-0{\cdot}5$ and $-1{\cdot}0$ are available as logarithms, square roots and reciprocals.

The practical importance of these transformations lies in the fact that they are species characteristics. In surveys, for example, once the transformation appropriate to the species has been found, all future samples can be transformed automatically. The philosophical significance of the law may well be in its implication that there are right and wrong spatial dispositions for each organism, including man, and that environmental pressures are likely to be greater on populations that depart from the species' characteristic pattern.

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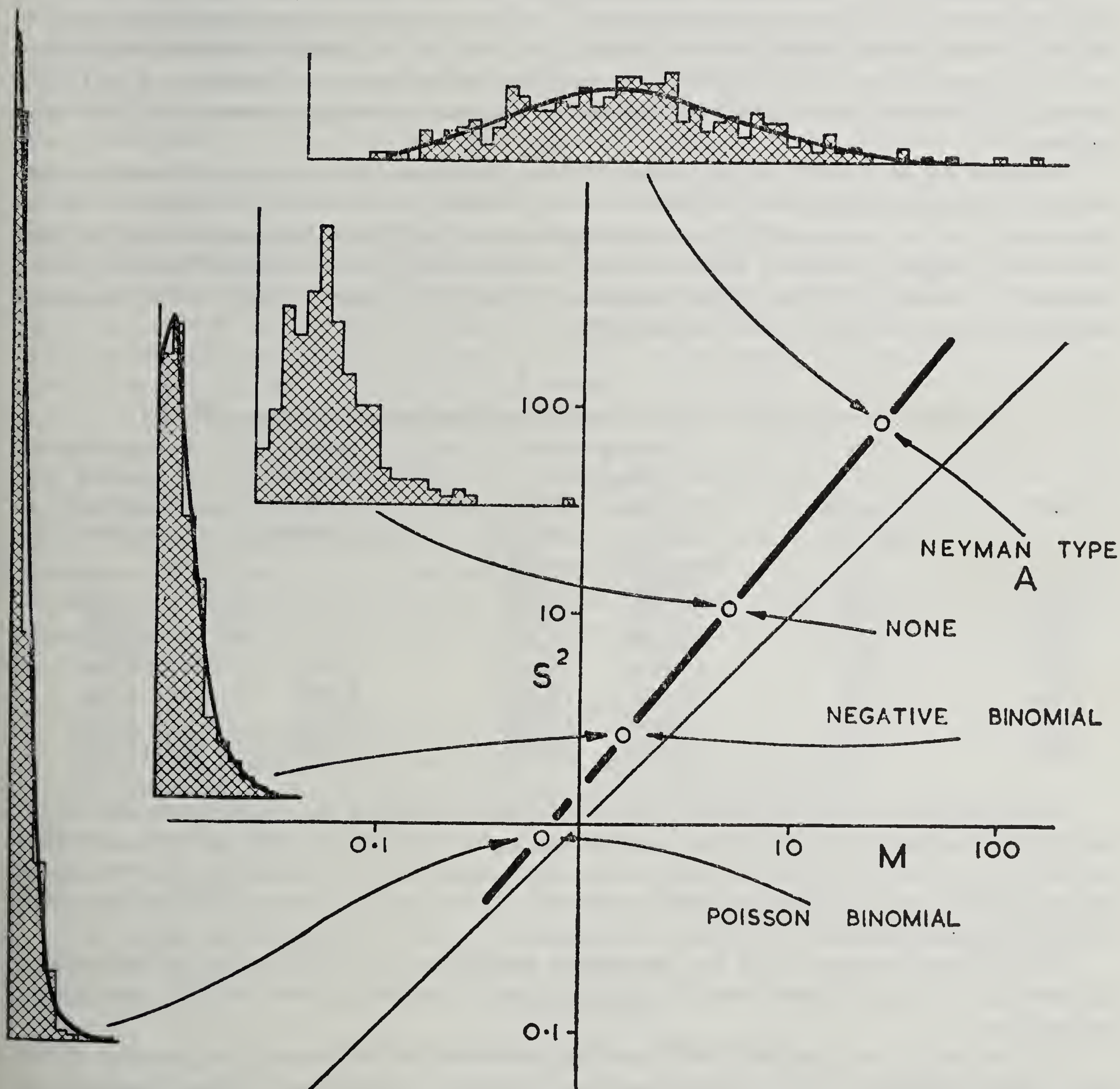

Fig. 1. 4 field samples of European Corn Borer: data from McGuire, Brindley and Bancroft (1957). 3 samples are perfectly fitted by 3 different distributions, the fourth by none. All four samples fit the expression $S^2 = 1{\cdot}5\ m^{1{\cdot}25}$.

SEX ATTRACTANT TRAPS WITH FEMALE ODOUR OF THE GYPSY MOTH USED FOR FORECASTING THE INCREASE OF POPULATION OF GYPSY MOTH

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The trap method used in Yugoslavia discloses the presence of very small numbers of gypsy moths and also serves for an uninterrupted study of change in population density. It is possible also to indicate critical density for best control results. The relationship between numbers of egg-clusters and numbers of males caught in traps was established. The average number of egg-clusters to every 25 males caught was 10/ha., while for 26 to 100 males it may go up from 10 to 100/ha., which is the critical number.

Results are given of the application of this method in an area with almost no control measures; these are compared with results obtained in areas where the trap method was applied, together with introduction of control at critical numbers.

The present study began when the second post-war outbreak of gypsy moth in Yugoslavia finished in 1957. Traps were used that year. The average number of males per trap, in localities where control measures were discontinued, was 38·2; a further decrease was noted in the following two years. Since 1961 the density has shown a marked increase and in 1962 it reached the critical number, which in 1963 was far exceeded, showing an average of 136·7males per trap.

Another region where the trap method was applied and where control measures were introduced, is an area of about 36,000 ha. of oak woods (*Quercus robur L.*). The result of the introduced control measures did not show a great drop in density because the critical point was never reached. Table 1 shows us that in the course of the whole 1957-1963 period considerable areas produced critical numbers of males in traps. Here control measures included dabbing the egg-clusters with DNOC.

Table 1

Density dynamics and suppression of gypsy moths in oak forests 1957-63

Year	*Total no. of traps*	*Area of forest (hectares)*		*Area of forest selected for control*	*Area where control had been introduced*
		Less than critical no. of ♂♂	*With critical no. of ♂♂*		
1957	148	14,000	15,600	—	257
1958	172	13,400	21,000	—	1,000
1959	165	19,800	13,200	—	12,942
1960	144	12,600	16,200	3,441	4,510
1961	143	15,600	13,000	4,633	4,000
1962	139	15,000	12,800	6,719	2,123
1963	132	3,000	23,600	15,249	15,249

It has not been found necessary to carry out control measures on all areas showing critical numbers of males, as gypsy moths were not present in the whole area of 200 hectares controlled by one trap. Table 1 shows in this way reduced areas, but the reduction of areas under control in 1961 and particularly in 1962, resulted in a noticeable increase in 1963 of areas with critical numbers of moths.

This evidently shows that a low population density during build-up may be maintained by carrying out control measures on the whole area containing moie than 10 egg-clusters per hectare.

In conclusion, the trap method is not only effective in discovering the presence of the gypsy moth in forests, but can also be used to study their population dynamics and critical point of density.

APPLICATION AND COMPARISONS OF MARK-RECAPTURE MODELS

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Mark-recapture sampling was carried out on two populations of the Queensland Fruit-fly *Dacus tryoni* in Sydney, Australia, as part of the research program of Dr. M. A. Bateman of the C.S.I.R.O. and Professor L. C. Birch of the University of Sydney. A preliminary paper (3) has already been published. The first population considered occurs naturally in a C.S.I.R.O. orchard near Wilton, New South Wales, and was sampled twice a week for nineteen weeks—from the time in the spring when it was first large enough to sample until its ultimate decline in the winter. The peak numbers during the summer reached about 23,000 adults and we usually succeeded in capturing, marking and releasing about 10-15% of the existing population. The data were analysed by means of three models: the Lincoln Index (1); Leslie's preliminary analysis (2) and a more complex model of Leslie's which may be called the "re-recapture" model. These models gave significantly different estimates of the population size during periods of extensive adult emergence. There was evidence that the newly emerged adults had much lower survival rates than did the older flies. Consequently, only the "re-recapture" model, which considers that different groups of marked flies may have different survival rates, could give reliable unbiased estimates at these times. Randomness of recapture of marked individuals was tested by several methods suggested by Leslie, Chitty and Chitty (1953). No deviations from randomness were detected. Randomness of capture of unmarked individuals was investigated by two methods: one comparing emergence rates estimated independently from the mark-recapture data and from pupal sampling data, and another which depended upon certain irregularities in the mark-recapture estimates of the sex-ratio. The latter suggested that, at certain times, the male flies were not captured at random.

The second population of fruit-fly was composed of four cohorts of adults liberated into field cages to investigate the possibility of adults overwintering in the Sydney area. These data were analysed by three methods, all assuming no dilution due to immigration or emergence. These were Leslie's no dilution Method A (p. 371), the approximate Method B (p. 378), and the full solution Method B models (p. 375), all from Leslie (1952). Because the data involved a chain of twelve weekly samples, the equation system of the full solution Method B model was solved and the variances evaluated on a digital computer. The approximate Method B was less affected by stochastic deviations of the real populations from the assumptions of the deterministic models than was the Method A model. The full solution Method B model, which gives much smaller values for the theoretical variances, is extremely sensitive to deviations from expectations and under certain conditions of population and sample size will give biased answers even when the only deviations of actual recaptures from expectation is due to the necessity that the numbers of recaptures must be integer numbers while the expectations may be decimal fractions.

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RULES GOVERNING THE COMBINED EFFECTS OF SUCCESSIVE MORTALITIES

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When a population of insects is affected, in the course of a generation, by a succession of different mortalities, the resultant effect depends on the types of mortalities involved, on how powerful they are, and in what order they act. Aspects of this subject have been dealt with by Thompson (1928, 1955), Bess (1945), and by R. F. Morris (1957), who reviewed the earlier

papers, and (in relation to their theory of parasite-host interaction) by Nicholson (1933) and by Nicholson and Bailey (1935); Varley (1947) applied the Nicholson-Bailey method to an actual example.

These papers deal with the matter in more or less complicated ways dictated by particular models or formulae. My purpose is to point out that the effects of successive mortalities can be dealt with by methods that are very simple in principle, and that some of the relationships involved can be summarised by elementary rules (not all of which seem to have been recognised).

The first point is that it is easier to combine survival rates than mortality rates: if one third of a population is killed by an early mortality and three-quarters of the remainder by a later mortality, the fraction of the original population surviving at the end is $2/3 \times 1/4 = 1/6$. This method was used in studies of spruce budworm populations (Morris, 1963).

Three different types of mortality will be considered: density-dependent, killing a higher percentage at high population densities than at low densities; density-independent, killing a percentage that does not depend on abundance; and "constant number" mortality, killing the same number of animals whether density is high or low—in the short-term view, the action of some natural enemies may approach this pattern.

Some rules governing combinations of these mortalities are set out below. They can readily be illustrated by simple arithmetical examples, with the aid of a graph of density-dependent mortalities from which survivals at different densities can be read (cf. p. 35 et seq. in Advances in Ecological Research, Vol. 2; Academic Press).

1. The final result of a succession of density-independent mortalities is not affected by the order in which they operate.
2. The final effect of two successive density-dependent mortalities is greater when the more powerful operates first.
3. If a density-dependent and one or more density-independent mortalities act in succession, the greatest final reduction is achieved when the density-dependent mortality acts first.
4. When a density-independent mortality precedes or follows a mortality killing a set number of individuals, the greater final reduction is achieved when the density-independent mortality comes first.
5. As 4, substituting density-dependent for density-independent.
6. In general, greater reduction is achieved when the mortalities more weakened (in terms of numbers killed) by a reduction of density operate before those less affected by density.

Complications affecting the operation of this principle in particular cases, such as changes in the susceptibility of insects during their development, must be dealt with according to the circumstances.

RECENT STUDIES OF SCRUB TYPHUS VECTORS IN MALAYA

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Recent studies of scrub typhus vectors in Malaya have been directed toward obtaining more information on the ecology of the vector mites of scrub typhus, with special emphasis on observations in their natural habitat.

The use of 4×5 inch black plates, placed five feet apart in transects, now allows the measurement of mite populations with the unit of measurement being the number of plates positive per transect or the mean number of mites per plate, or both. The additional use of a one foot square frame, especially in the forest, allows a random counting of the numbers of clusters, which gives a measurement of the population similar to that found with black plates. The black plates are the most effective and practical method of locating and assessing mite populations in this area.

The use of black plates in transects has clearly shown a habitat difference between *Leptotrombidium* (*Leptotrombidium*) *deliense* and *Leptotrombidum* (*Leptotrombidium*) *akamushi*, the two

primary vectors of scrub typhus in Malaya. The former is restricted to forest and the latter primarily to areas dominated by lallang grass. This evidence shows a clear biological difference that supports the morphological separation of these into two distinct species in Malaya.

A series of twenty transects of thirty black plates each, located in lallang grass, scrub and secondary forest, have been operated on a weekly basis for sixty-seven weeks to obtain information on mite populations. The results have shown a higher population in the winter months during the period of highest rainfall with a direct correlation between rainfall and larval populations.

The location of foci through the use of black plates has led to the observation that larval mites of the vector species cluster approximately three inches above the ground on dead grass stems, leaves and twigs. The clusters remain for up to three weeks in the same location, and are found in the same place both at night and during the day. There is a reaction to any foreign object placed near the clusters except when the temperature rises and the humidity goes down in the late morning and the mites become less responsive. The mites do not actively seek the host but wait in clusters for the host to come into contact. Clusters are larger and more abundant during periods of heavier rainfall, however very wet as well as very dry conditions are detrimental to clustering.

Further studies are currently underway to obtain more information on chigger production, the duration of foci, the clustering, the reproductive ability in colonies, the longevity of post-larval forms and reactions to light and other physical factors. Studies of the host animals are also being conducted with the use of miniature transistorised radios.

MICRO-CLIMATE AND OTHER ENVIRONMENTAL FACTORS AFFECTING RANGE AND DISTRIBUTION

HABITAT CHANGES BY INSECT AND OTHER TERRESTRIAL ORGANISMS AS AN ECOLOGICAL PRINCIPLE

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Each species occupies a characteristic complex of habitats, but former ideas on the constancy of choice are too formal and contradict too many new facts. Habitats are often determined by microclimate and can undergo pronounced changes in the wide range of space and time. These form our principle of the change of habitats (1957, 1959, 1962), which is a complex of phenomena, manifested in space as zonal and vertical change of stations and as zonal change of strata. In time it is manifested as seasonal and annual change of stations.

Zonal change of stations is typical of widely distributed species: in the north of their range they prefer dry, warm situations with sparse vegetation, but in the south more humid and shady places with dense vegetation (Bey-Bienko, 1930, 1959). This type of habitat change is characteristic of many insect species, e.g. the locust *Calliptamus italicus* inhabits dry sandy places and chalk hill slopes with sparse vegetation in the north, whilst in the south it lives in river valleys, oases and foothills (Bey-Bienko, 1941). Vertical change of station is similar to zonal, but is seen in mountains; e.g. the grasshopper *Decticus verrucivorus* prefers meso- and hygrophitic stations in the Caucasian forest belt, but xero- and mesophitic ones in the alpine belt. Zonal change of strata (Ghilarov, 1951) is expressed by trans-zonal species occupying different strata in different zones; some terrestrial species become at least partially soil dwelling in dry zones, others when dispersing northwards move from a higher vegetation stratum to that near the ground.

Change of habitats in time is due to alterations of microclimate in one or several years. Seasonal movements are especially marked in regions with a warm climate and pronounced seasons; e.g. steppe and desert insects migrate to crops, river valleys, damp meadows and woods during a summer drought (Sakharov, 1947). The alternation of dry and rainy seasons in tropical Africa contributes to change of stations in several Acridoidea species (Davey, 1956, 1959; Phipps, 1959). In Siberia, Kazakhstan and other parts of USSR many Acridoidea migrate in summer to sites with denser cover, returning in autumn to their former stations (Bey-Bienko, 1928; Ratanov, 1941, Rubtsov, 1932; Stebaev, 1957). Annual change of stations occurs as a result of a sharp alteration of weather over several years; in drier and warmer years a species migrates to the stations with a higher degree of moisture, in cool and moist years it moves to warmer stations. For example, *Locusta migratoria* in southern Kazakhstan concentrates in dry years in depressions with more humid soil and dense vegetation cover, where it lays its eggs; in more humid years higher, dry sites are chosen (Tsukerman, 1960). In dry warm years migrations of many insect species to moister stations were observed in the Ukraine, and a reverse effect is seen in moist and cool years (Kryshtal, 1954).

As a whole, the principle of the change of habitats reflects complicated dynamic interrelations between the species and its environment. The biology and ecology of many species cannot be understood without taking into consideration the change of habitats. Without this understanding the development of necessary practical measures to control injurious species and to promote beneficial ones will encounter difficulties and even result in serious errors.

THE INFLUENCE OF MICRO-CLIMATE ON THE DISTRIBUTION OF STORED PRODUCTS INSECTS

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When an insect can be studied both in its natural habitat and in the laboratory it is natural to expect some correspondence between the results. If the laboratory experiments appear to explain the field observations then it is tempting to attempt to extend the laboratory work to predict the probable outcome in the field in conditions not often directly observable. This is especially inviting for the worker with stored products insects since these can be bred in the laboratory in conditions which seem to be very similar to those in warehouses and this natural environment appears to be relatively simple and on the whole fairly constant.

At the outset it is probably worth pointing out that the warehouse environment is considerably more complex and variable than it seems and that conditions in laboratory cultures are usually very different from warehouse conditions and that some storage insects are very difficult to breed in the laboratory.

The warehouse environment comprises two quite different habitats, the stored foodstuffs in which conditions are usually equable but sometimes very warm, and the surfaces of the food and fabric where the conditions may change regularly and considerably. Many species live close to the boundary between the two, and one stage may be spent in the food and the other out of it. On the whole laboratory cultures are much more dense than warehouse populations.

In practice, our earliest laboratory work merely showed that the established pests were capable of very rapid rates of population growth and that the less abundant species were hampered by slower developmental rates or a diapause, or laid very few eggs, at least in laboratory culture. However, for the spider beetle *Ptinus tectus*, a temperate species common only in the damper regions of N.W. Europe, New Zealand and British Columbia we attempted to map its potential range. One of its predicted probable niches was the Kenya Highlands so it was most gratifying that Coombs and McFarlane should find a couple of years ago that the species was quite common there. However, apparent failures of a theory are much more interesting and instructive. The only instance of this encountered to date was the widespread occurrence of the tropical saw-toothed grain beetle *Oryzaephilus surinamensis* in Britain and Scandinavia. Laboratory experiments showed that this species would not develop at temperatures below 18°C and I would have predicted that it would not thrive below 22°C. There were, however, many farm and warehouse observations of hot spots containing only this species embedded in very cold grain, so that field workers inferred that the species had bred in grain at 10-15°C. Studies arising from these observations showed in fact that modern harvesting methods had often provided this beetle with grain initially at temperatures between 25 and 35°C, often damp and dusty also. Thereafter the beetle bred but the grain cooled and if the beetles grew fast enough and produced enough heat a hot spot developed in a mass of cooler grain.

It is worth looking at some of the defects of this type of prediction. Firstly the laboratory studies yield from a mathematical formula, a figure for rate of increase which is something of a fiction. It assumes a stable age distribution which probably never exists in warehouses. However, it does represent the potentiality of the species for a rapid initial increase.

Secondly the laboratory investigations at constant conditions must be related to the field conditions. Often our idea of these are outdoor meteorological readings, perhaps only monthly means. Anything but very broad conclusions drawn from these would be sheer optimism. Given a fairly accurate record of warehouse conditions, a reasonably confident prediction of rates of multiplication can be made for a range of 10° from just below the optimum. Outside this narrow range, some concentrated experimentation is still needed to elucidate the effects of small doses of high and low temperature. The maxima and minima obtained from constant temperature work are too conservative. Growth proceeds at temperatures below the constant temperature minimum, so if the temperature falls below this level regularly, the insect will grow faster than the data would predict. On the other hand, short spells of a week or two at such a temperature might be fatal to some stages.

MICROCLIMATE AND DESERT ADAPTATION IN ARTHROPODA

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Desert climates are characterised by extremes of temperature and humidity, low, irregular rainfall and strong winds which not only increase the drying effect of the air but carry dust and fine particles of sand. Soil surface temperatures often reach an extremely high level, 84°C (183°F) having been recorded on a number of occasions. A short distance beneath the surface, however, the climate becomes progressively more stable. For example, below about 50 cm. there is hardly any diurnal temperature variation in the sands of the Sahara. Consequently burrowing is the most important behavioural adaptation of arthropods to hot-dry environments and the existence of favourable microclimates within the burrows of desert animals is of supreme importance to their survival. Scorpions and Solifugae, for example, make deep excavations in the ground, the latter often closing the entrance with a plug of dead leaves.

Many desert arthropods confine their activities to the hours of darkness when the temperature is lower but some, such as grasshoppers, ants and tenebrionid beetles may be active during the hottest part of the day, many of them having long legs which raise their bodies above the scorching sand. In addition to diurnal rhythms, many desert arthropods show seasonal rhythms and survive unfavourable periods in diapause which is broken by the onset of rain.

Desert arthropods may sometimes obtain moisture from dew or hygroscopic vegetation, but are usually able to exist independently of this. Water-loss by transpiration in desert forms is much lower than in related species from more humid environments. Some species are probably able to absorb moisture from unsaturated air through the integument, water is obtained from food and metabolic water conserved. In addition, desert arthropods show an enhanced ability to survive desiccation.

Many desert animals can survive exposure to extremely high temperatures, the "camel-spider" *Galeodes granti* Pocock and the scorpion *Leiurus quinquestriatus* (H. and E.) surviving 50°C and 48°C respectively for 24 hours at a relative humidity below 10 per cent. Heat death in these animals and among desert beetles has been shown to be correlated with a decrease in blood pH suggesting that it may be associated with the accumulation of acid metabolites.

The colours of desert animals have long been a matter of interest and their function of dispute. Most arthropods are either black, resulting from Müllerian mimicry, or else pale and cryptic: dark colours do not result in greatly increased heat stress. The sub-elytral cavity of beetles reduces transpiration though the air within it is not humid.

Desert arthropods show a surprising resistance to prolonged starvation, a high proportion of species being either carnivorous or omnivorous. The basis of food chains in areas devoid of plants consists of dried vegetable matter blown from elsewhere. The adaptations of desert arthropods to their environment represent changes in degree rather than in kind. The desert fauna has been derived from the inhabitants of less extreme habitats whose physiology and behaviour pre-adapted them to the colonisation of arid regions.

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CONNECTION OF INSECTS WITH THE SOIL IN DIFFERENT CLIMATIC ZONES

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Air in soil is at some depth saturated with water vapour, thus soil can be considered as intermediate between aquatic and purely terrestrial habitats. The phylogenetic transition of many groups of invertebrates from aquatic to terrestrial life took place through the soil because air breathing in the soil is possible without significant loss of water (6, 9). Many groups of land invertebrates still insufficiently adapted to resist desiccation are soil dwellers. Insects represent the invertebrate group best adapted to resist loss of water, but the degree of adaptation is different in various groups of insects and the danger of desiccation is different in various climatic conditions. The adult stages of Pterygota are better adjusted to resist desiccation, the larvae being connected with habitats where air humidity is near the saturation point—especially with the soil.

Many insect species inhabiting suprasoil parts of plants in wet periods become subterranean in dry ones (3). When the range of the species overlaps different climatic zones the development of the insect in the humid zones proceeds on the suprasoil parts of plants, whereas in the arid ones the species becomes a soil dweller (10). In many orders, families and genera, those species which are distributed in humid zones develop in or on aerial parts of plants, whereas in arid zones species belonging to the same taxonomic group are soil dwellers (e.g. termites, Tenebrionids, longicorn beetles). This "Rule of the Zonal Change of Strata" (7, 8) is closely related to the wider "Rule of the Zonal Change of Stations" (1, 2).

In very humid conditions (tundra, rain forests, caves) representatives of the soil fauna leave the soil stratum, whereas in arid zones (steppes, deserts) there are many insects which are secondary adapted to soil dwelling. The more humid the zone, the nearer to the surface are insects and other animals connected with the soil and so the humus horizon (A_1) is but feebly developed.

In tundra many soil insects are active during the summer not in the soil, but above the soil surface between moss plants. Correspondingly, the soil layer is very primitive and underdeveloped. In taiga, in coniferous forests, soil animals are active in the litter and very uppermost soil layer, causing the absence or very feeble development of horizon A_1 in podsols. In semi-podsols in the zone of mixed forests insects and other soil dwellers are active during the drier warm months, some migrating down to 10-25 cm to escape desiccation and, correspondingly, horizon A_1 is so deep in these soils.

"Gray-forest soils" are formed in deciduous forests and forest-steppe zones where the surface soil dries out in summer and downward migration of soil dwellers causes horizon A_1 to reach as much as 40 cm deep. Equally in steppe zones downward movement of invertebrates causes rich black humus to extend as far as 100-120 cm deep.

In deserts the humus content is negligible but the feebly humified layer may reach down to 2 metres—the depth of soil insect migration. In the same latitudes, in humid forests the soil strata are similar to podsols because lack of oxygen keeps soil animals near the surface.

Finally, the depth of humus distribution and the depth of soil animal migration are reciprocally interdependent (5, 7, 8) and often depend on drainage and aeration.

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L'ENTOMOFAUNE DANS LE SOL DES PATURAGES SUR LE SOLONETZ ET SUR LE SABLE

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Ces recherches ont été poursuivies pendant l'automne 1963, dans la province de Voïvodina (nord-est de Yougoslavie) caracterisée par une variété particulière du climat semi-aride steppique du sud-ouest. Les échantillons ont été prélevés dans deux pâturages, se trouvant sur des types de sols différents. La grandeur des échantillons a été de 0,25-1,00 m^2, à 50 cm de profondeur. Il a été examiné sur le sable un total de 79 m^2/79 échantillons/et sur le solonetz 27 m^2 (108 échantillons).

L'entomofaune du pâturage sur le sable est, au point de vue quantitatif et qualitatif, bien plus pauvre, en comparaison à celle du pâturage sur le solenetz, ce dernier type de sol assurant un milieu plus favorable pour la vie des insectes. Il a été trouvé sur le sable 10,5 et sur le solonetz 46,5 examplaires de macro-entomofaune par m^2, dont 80-83% appartiennent aux coléoptères. Sur le sable, ce sont les Scarabaeidae qui prédominent, avec 92,3% de tous les insectes de Coleoptera recueillis; sur le solonetz ce sont les Elateridae (30,9%), les Cerambycidae (23,1%), les Tenebrionidae (16,6%) et les Scarabaeidae (16,0%).

Dans le sol du pâturage sur le sable la présence des espèces ou genres suivants des coléoptères a été constatée: *Tentyria nomas* Pall., *Opatrum sabulosum* L., *Blaps halophila* Fisch., *Anoxia pilosa* F., *A. orientalis* Kryn., *Anisoplia deserticola* F., *A. segetum* Hbrst., *Anomala errans* F., *Maladera holosericea* Scop., *Polyphylla fullo* L., *Homaloplia* sp., *Harpalus frölichi* Sturm. (et probablement *H. psittaceus* Geoff.), *Acinopus* sp. Des espèces mentionnées sur le sable prédominent les suivantes: *Tentyria nomas* Pall., *Anisoplia deserticola* F., *Anoxia pilosa* F., *A. orientalis* Kryn.

Dans le sol du pâturage sur le solonetz les espèces ou genres suivants des coléoptères ont été déterminés: *Limonius pilosus* Lesce., *Agriotes sputator* L., *A. brevis* Cand., *A. sordidus rufipalpis* Brullé., *Melanotus punctolineatus* Pell., *Selatosomus latus* F., *Crypticus quisquilius* L., *Opatrum sabulosum* L., *Anisoplia austriaca* Hrbst., *Anisoplia* sp., *Aphodius* spp., *Rhizotrogus aequinoctialis* Hrbst., *Amphimallon solstitialis* L., *Pentodon idiota* Hrbst., *Eusomus* sp., *Sitona* sp., *Dorcadion pedestre* Poda., *D. fulvum* Scop., *D. scopoli* Hrbst., *Neodorcadion bilineatum* Germ., *Harpalus affinis* Schrank, *H. pygmaeus* Dej., *H. aeneus* Fbr., *H. rubripes* Dft., *Amara aenea* Deg., *Ophonus azureus* F., *Stenolophus* sp., *Galeruca* sp. Des espèces mentionnées sur le solonetz prédominent les suivantes: *Limonius pilosus* Lesce., *Crypticus quisquilius* L., *Anisoplia* sp. et les espèces du genre *Dorcadion*.

THE EFFECT OF ENVIRONMENTAL TEMPERATURE ON THE ECOLOGY OF *HELIOTHIS ZEA*

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In the ecosystem concept living organisms and their non-living environment are interrelated and interact upon each other. Our present concern is the effect of one factor of the physical environment, temperature, upon the ecology of one insect—*Heliothis zea*. There has developed a need for a more definite term than micro-environment, micro-climate, etc. The terms which are now becoming generally acceptable to most agro-meteorologists and biometeorologists are the bio-climate as measuring the physical state of a particular bio-sphere which encompasses the total physical environment of a particular living organism. The bio-climate of the corn earworm thus includes the first several inches of the soil and the lower

1000 feet or so of the atmosphere. Generally, an insect bio-climate would cover the bio-sphere of that particular insect which would include that portion of the earth and the atmosphere in which the particular insect ranges.

Temperature observations taken with reference to corn earworm environmental studies have previously been recorded in standard cotton region shelters placed adjacent to a corn field. These data would more nearly represent the human bio-climate rather than the bio-climate of the corn earworm. To measure the actual temperatures in the earworm's bio-sphere, thermistor probes were placed at ecologically important locations within a corn plant in a mature corn field. Temperatures were taken in the corn whorl, the corn silk, between the leaf and stalk, on the surface of the stalk, in the air 36 inches above the ground, and under two inches of soil at the base of the stalk. The averages obtained were highly variable during daylight hours, depending on the position of the plant in relation to the sun, and showed less variability during the night. Ear tip and soil temperatures were considerably higher than air temperatures. Using data of earworm catches at the adjacent light trap a hypothetical generation (from peak to peak of light trap catch) was developed. This hypothetical generation would have been subjected to the following average temperatures during the different stages: mating and egg laying, 26·1°C; egg hatching, 26·9°C; larval feeding, 25·5°C; pupation, 27·3°C.

Larvae reared under conditions of continuous light, humidity and temperatures do not attain as high a rate of survival as those reared under variable conditions. The data collected in this portion of the study on environmental factors affecting the ecology of *Heliothis zea* would indicate that under natural environmental conditions the insect is subjected to large variations in environmental temperatures both within and between stages. This would indicate that a higher survival rate of laboratory reared insects might be obtained if rearing chambers were programmed to produce diurnal changes and changes from stage to stage.

PHYSIOLOGICAL ASPECTS OF ECOLOGY

ECONOMY OF GROWTH IN *HYLOTRUPES* (COLEOPTERA) AT DIFFERENT ECOLOGICAL CONDITIONS

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The larvae of the House Longhorn beetle, *Hylotrupes bajulus* L. live in seasoned softwoods and are serious pests of structural timber. They grow only slowly in natural seasoned wood, and as breeding is important for test purposes, growth responses to several factors have been studied: enrichment with peptones and yeast extract, temperature, and humidity.

Considering the well-established responses to these factors I formulated the question: When the larvae grow faster at certain conditions is it because they gain more in larval weight per unit weight consumption or is it because they eat more per unit time?

The growth of the larvae was studied at constant conditions and it was found that in the proper growth period the growth is exponential (=logarithmically linear) until the larvae prepare for metamorphosis at about 200 mg of weight. The ratios between the weight, the consumption, and the amount of boremeal were practically constant during the exponential growth.

The logarithm of the weight/consumption ratio was called the economy of growth and it was analysed as a function of the log. weight. Economy of growth was highest in the biggest larvae within groups of equal aged larvae kept at constant conditions, but it was lower in older and bigger larvae than in younger. The decrease of economy with age was very slow during exponential growth.

Economy of growth was used for analysing growth response to variations in ecological factors. Considering increasing rate of growth with increasing doses of peptone below the optimum it appears that increasing rate of growth is caused by a better economy of growth. However, with further increasing doses there is an optimal dose above which the growth rate decreases again, but economy of growth was steadily increasing even beyond the growth optimum. It thus follows that the slower growth rate at higher doses of peptone must be caused by a lower rate of consumption.

With increasing relative humidity the larvae steadily grow faster and comparing the speeding up of the growth by increasing dose of peptone with the response to increasing RH it appeared that with increasing RH the increasing growth rates were caused by higher rates of consumption and not by a better economy of growth.

With increasing temperatures there is an optimal level too, but unlike the effect with peptone the economy of growth is steadily decreasing, and the increase in growth rate in the lower region of the temperature range must therefore be caused by an increasing rate of consumption which cannot keep step with the falling economy of growth at higher temperatures.

Finally the response to varied doses of cholesterol showed a typical optimum and the curve coincided roughly with the variation in the economy of growth showing that the rate of consumption was constant relative to the weight of the larvae.

Economy of growth was used to explain the result of an experiment where growth did not increase with relative humidity at very high levels. A lower economy of growth was found at the highest level and this indicated that some of the peptone had been lost and this was further rendered probable by the observation of a heavy growth of mould solely in that particular group.

Economy of growth might be used to analyse more complex sets of ecological conditions, e.g. current problems in applied ecology of *Hylotrupes*: response to ageing in structural timbers beyond 50 years, and effect of heat treatment on timber as food for *Hylotrupes*.

I realise that the scope of this communication is not physiological in its causality, but it was intended to provoke comments on the rôle of this type of causality in ecology.

IMPORTANCE DE LA PHOTOPERIODE PENDANT LA PONTE DE 3 RACES DU CRIQUET MIGRATEUR

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Différents mécanismes règlant le developpement embryonnaire sont généralement retenus pour les 3 groupes sous-spécifiques de Locusta rencontrés en France (1).

Au cours de la vie d'une population dense de Locusta, l'aptitude à produire des oeufs à diapause diminue, toutes conditions égales par ailleurs (température des élevages, d'incubation, nourriture, durée d'illumination) sauf la densité de la population, décroissante. Cet "effet de vieillissement" est observé sur les souches indiquées ci-dessous et pour les tendances plus poussées favorables à la diapause (Katakstan) ou à son absence (Sardaigne). Cette observation, sur 4 races est valable pour des photopériodes de 8, 10, 12, 14, et 16h.

Lorsque les Locusta des souches ci-dessous sont soumis aux conditions d'illumination de la latitude 49°, le chauffage d'appoint étant apporté dans les limites de l'éclairage du solstice d'hiver, l'évolution de la proportion des oeufs en diapause se fait selon deux modalités (4).

(1) entre le solstice d'été et l'équinoxe d'automne: augmentation.

(2) le reste de l'année: diminution, selon la même pente que celle correspondant au "vieillissement".

Les limites, marquant ces inflexions, sont éventuellement décalées en fonction del'apti tude moyenne de la souche et de l'âge de la population lorsqu'elle franchit ces périodes.

(*a*) Ce genre d'interactions a été plus spécialement étudié sur la forme "de Palavas", à partir de lignées indépendantes. Des sélections, opérant comme il a été montré sur une autre race (1), permettent, après 17 générations, de disposer d'une centaine de documents couvrant toute l'année. Avec le maintien de l'instabilité (sélections opposées selon les générations), il est ainsi possible de couvrir un graphique, y compris les zones 0–15% et 85–100% de diapause. Les deux inflexions signalées s'y retrouvent, et elles seules.

(*b*) Les mêmes résultats sont obtenus pour les souches provenant du littoral languedocien, à l'ouest de la répartition—limite de "Palavas": St. Pierre, Vendres, et à l'est: Grau-du-Roi, Stes Maries, Beauduc, Fos. Le niveau moyen de réponse est du même ordre que pour a (*a*).

(*c*) Même résultat avec *L.m. gallica* de deux stations septentrionales. Cependant, la démonstration demande l'utilisation de plusieurs générations de sélection anti-diapause pour permettre l'obtention de niveaux de diapause superposables à ceux de (*a*). Ces lignées ont au départ une aptitude sensiblement plus élevée à la diapause (E. Vannes, Carnac) que celles de (*d*).

(*d*) *L.m. gallica* méridional (Audenge, N. Bayonne) se comporte de la même façon.

(*e*) Enfin, des insectes provenant de Hyères et considérés comme répresentant *L.m. cinerascens* (3) montrent, même incubés à 31°C une faible proportion d'oeufs à diapause. Ce point est nouveau (2) et, en fait, 300km plus au sud, nous trouvons encore une telle aptitude pour de plus faibles températures. Ici encore, la sélection est possible. Le seul moment de l'année ou cette souche, non sélectionnée, produit effectivement ·0% d'oeufs à diapause est la période où l'illumination dépasse 13h 15. En-dessous, les courbes représentant l'évolution des pontes sont du même type que précédemment.

Appartenance à une race et origine latitudinale ne font que décaler les proportions des deux types d'oeufs, lesquelles évoluent identiquement vis-à-vis du facteur photopériodique. La période de ponte effective dans nos régions correspond à une évolution particulière dans l'ensemble de l'année.

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THE ACTIVITY OF BENTHIC INSECTS IN THE WATER MASS OF LAKES

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Intensive use of a new type of emergence trap has established the pattern of seasonal emergence of Diptera from different depths in Esthwaite Water, a productive lake in the English Lake District. The traps have been used to catch both ascending and descending insects and they have demonstrated very extensive vertical movements of larvae from the sediments into the overlying water. The most abundant larvae were those of *Procladius*. In April in mid lake these were caught at the rate of 50 larvae/sq.m./day 1 metre above the mud, and 10/sq.m./ day 10m above the mud (5m below the water surface). Larvae were also caught, but in smaller numbers, nearer the shore. Catches continued through the summer, especially in June, but numbers declined in later summer and autumn. Other genera show different patterns of activity. *Chironomus anthracinus* Zett. was caught in greatest numbers from mid-August to the end of October especially near the sediments at 7m; *Sergentia coracina* Zett. moved vertically in the middle of the lake in June and July but as summer advances it is found in shallower water. Larvae of *Endochironomus albipennis* Mg. were caught above the littoral from May to October. These larvae, therefore, although clearly adapted for burrowing, make extensive vertical migrations which are probably related to the seasonal cycle of stratification and de-oxygenation in the bottom waters of the lake, since ascent takes the larvae out of the zone where oxygen is lacking. The Orthocladiinae in the littoral, however, also exhibit the movements.

These findings show that the fauna of the mud may be only partially sampled by mud samplers, and that much of the benthos must be constantly available to fish as food. This explains the frequent occurrence in the stomachs of fish of larvae free from mud. Also, although experimental work on the respiration of *Chironomus* larvae has shown that some species can survive the absence of oxygen for several weeks, it is now clear that under natural conditions they need not depend on this ability, since they can move up into aerated waters. It must be noted that these catches of larvae are to be distinguished from those of early instar larvae seeking optimum habitats after hatching, and from catches of species carried into deep water by waves after being dislodged from the shallows, or by density currents from inflowing streams after heavy rain.

THE DISTRIBUTION AND PHYSIOLOGY OF SOME LAKE CORIXIDAE

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Corixidae have been collected from a large number of water bodies in central British Columbia. The same species do not occur in every habitat and all habitats do not have the same chemical composition. A correlation between Corixid distribution and salinity is found. Even if salinity does not govern the distribution of the species studied, at least it is a major factor in the environment and one with which the animals must contend.

Attempts have been made to find experimentally how the insects are able to survive should they enter a water body other than that in which they developed. There are many records of aerial dispersal of Corixidae and the apparent invasion of available water bodies indiscriminately. The lakes studied are close together and within the range of the four species which received special attention, namely *Callicorixa audeni* Hung., *Hesperocorixa laevigata* (Uhler), *Cenocorixa bifida* (Hung.) and *C. expleta* (Uhler).

Adult Corixids were transferred from one lake water to another in order to study and measure various changes within the insect. We have studied: mortality, respiratory rate, locomotory activity, freezing point depression of haemolymph, Na, K and Cl levels in the

haemolymph, water content of the body, drinking, egg production and resorption, changes in the gut epithelium, and wing muscle polymorphism.

Space does not permit a detailed consideration of the methods and results. In summary, it appears that the species studied cannot live in all the lakes available in their range. They cannot tolerate all salinities without some marked effect. All four species are subject to considerable physiological stress when placed in waters other than those in which they developed. The more dissimilar the waters, the greater the physiological stress. Death in the most saline waters is associated with dehydration, uncontrolled drinking, drastic changes in ionic levels of the haemolymph and degeneration of the midgut epithelium. The two closely related species, *C. bifida* and *C. expleta*, do not maintain the same levels of anions and cations in the haemolymph when in the same medium. This suggests a fundamental physiological divergence which has resulted in a different distribution.

The results indicate that salinity is an important factor in the environment of these freshwater Corixidae, but no particular ion can be signalled out as all important. Salinity denies some lakes to the species studied and the magnitude of this environmental factor in other water bodies depends on the characteristics of the medium in which the insects developed.

Our other experiments on changes in the ovary and flight muscle polymorphism substantiate the fact that the environmental conditions under which the Corixids developed are all important in determining the success in any given water body which they might colonize. Thus, the success of the species in a given water body depends on the proportion of the population remaining in the habitat and the previous history of the new immigrants.

ON THE INFLUENCE OF SOME FOOD SUBSTANCES ON SURVIVAL OF CORIXIDAE (HETEROPTERA)

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In the literature on the food of Corixidae, members of the subfamily Corixinae are said to be largely plant and detritus feeders. Selected food substances were offered to some corixid species to see their effect on survival.

In August and September 1961, 26 experiments were started; in 23 of them unidentified adults or larvae-*V*, kept in running tap water, were amply supplied with one of the following food substances: *Tubifex*, daphnids, chironomid larvae, dead fresh water animals, waterplants, living or decaying algae, natural or laboratory made detritus. As a control, in three cases no food was available.

As a measure for the significance of a particular food, the daily mortality was plotted per species. It appeared that the shape of the curves for animal food was generally the same. Likewise, those for feeding on all types of plant material showed much resemblance, but were very different from the former.

In fig. 1 curves of experiments with comparable food are combined and given per species. The numbers of bugs fed on a type of food are presented in the table. In this figure an arrow indicates living specimens in an experiment after it was concluded; these bugs were killed.

Experiments with larvae of *Sigara distincta* (Fb.) are shown in fig. 2, and the number of larvae per experiment is given in brackets. The curves end on the day that all larvae had either died or moulted, so the remaining percentage all moulted to adults. Larvae of some other species were tested in small numbers but the results all show similar tendencies.

Feeding on algae and waterplants, as well as on detritus, usually gives similar mortality curves in all species. Moreover, there seem to be no, or only minor differences between feeding on plant materials and not being fed. Most species tested in control experiments were present in small numbers only, except for *Corixa punctata* (Ill.) and *S. distincta* larvae. Both curves are nearly identical with the corresponding curves for feeding on plant material.

It is obvious that in both adults and larvae of several species, survival is higher when feeding on animal food, and there does not seem to be much difference between the various types. Dead animal food, however, causes a higher mortality than living, not only in *C. punctata* (fig. 1A), but also in adults of *S. distincta*.—This food has not been tested on larvae.— This mortality may be induced partly by the unfavourable conditions created by the many

dead chironomids etc. required for supplying the bugs with ample food.

Chironomid larvae proved to be less favourable food for fifth instar larvae. It is likely that the sizes of prey and predator are of importance here, as the chironomids taken were generally much larger than the bugs.

Daphnids are likely to be an adequate food, and they appeared to be easily taken by both adults and larvae.

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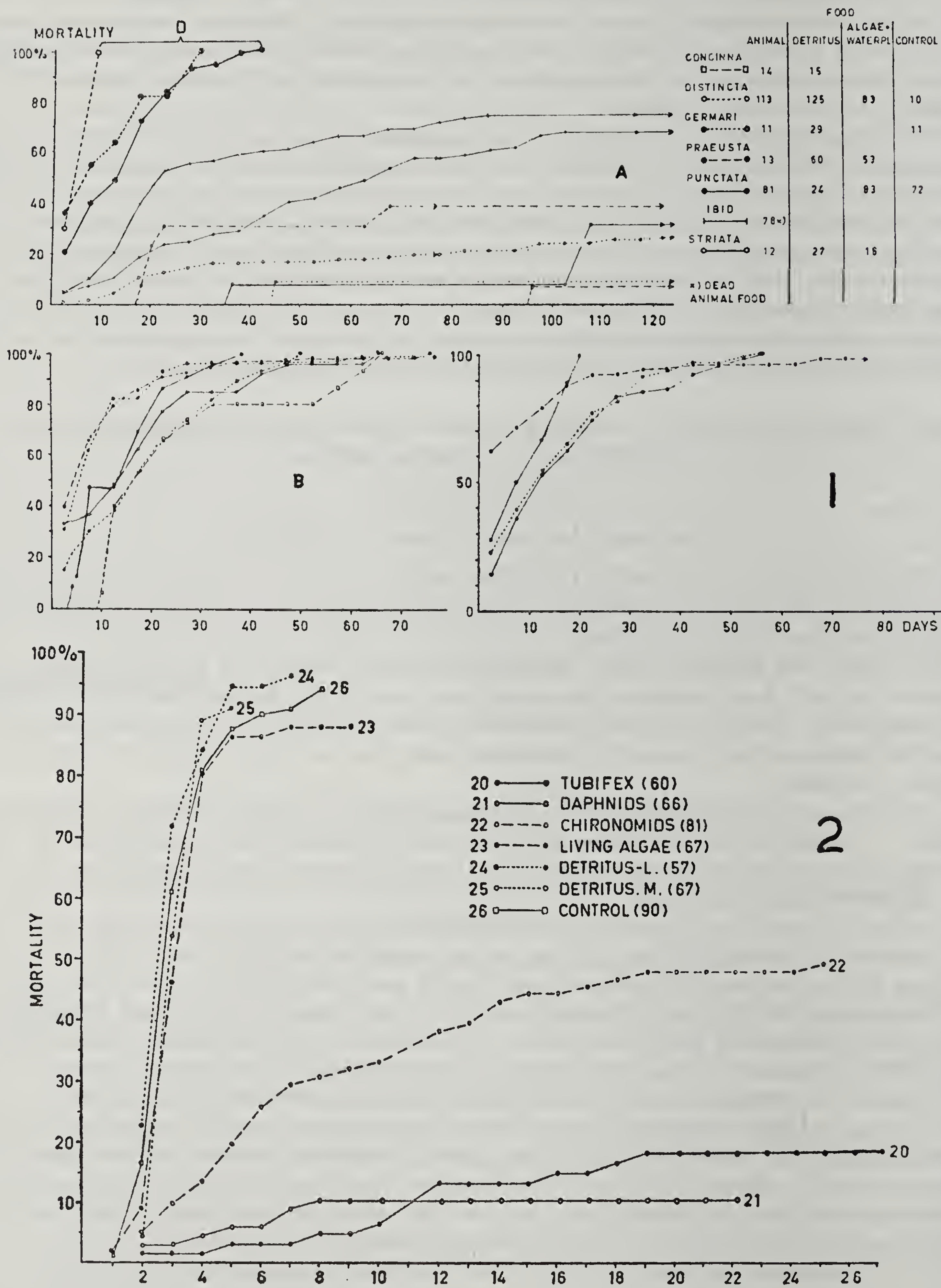

FIGS. 1-2.—Mortality of Corixidae. (1) Adults of *Arctocorisa*, *Callicorixa*, *Corixa* and *Sigara*, feeding on: A—animal food, B—detritus and decaying algae, C—living algae and waterplants, D—control (no food); (2) Larvae -V of *S. distincta* feeding on various foods.

THE PHYSIOLOGICAL SUPPRESSION OF INSECT PARASITOIDS

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Although the elimination of supernumerary larvae of solitary insect parasitoids has been known ever since work began on the biological control of insect pests at the end of the last century and frequently mentioned in the literature, the precise nature of the mechanism of the competition has not been fully investigated. Using the solitary Ichneumonids *Horogenes chrysostictos* and *Nemeritis canescens* (Hymenoptera) which parasitise larvae of *Ephestia kuhniella* (Lepidoptera) it has been shown that competition occurs both by physical attack and by physiological suppression of one parasite by the other. The two mechanisms occur both in superparasitism and multiparasitism by these species and their occurrence depends upon the difference in age between them (1). The phenomenon of a physiologically mediated suppression has received a variety of explanations; such as the secretion of some toxic substance by the survivor and the production of a cytolytic enzyme which destroys its competitors. But none of these explanations has been accompanied by any experimental evidence of its validity.

In a critical examination of physiological suppression (2) it has been demonstrated, first, that the suppression is mediated by the host's haemolymph and secondly, that although the haemolymph is made unsuitable for the development of subsequent parasitoids it is not permanently changed and the inhibiting factor is connected with the presence of a living parasitoid. In investigating the possible effects of the parasitoid's own metabolism as a means of exerting suppression of competitors it has been found that respiration is critical, since the availability of oxygen to the host controls the outcome of parasitic competition. The normal result of the competition is for the younger one to be suppressed and for the older to survive. However, by raising the oxygen content of the atmosphere surrounding the host and hence increasing the oxygen tension of its haemolymph proportionally, it is possible for the younger one to survive as well. By using this method of controlling the oxygen tension of the blood surrounding the parasite, it has been possible to simulate the physiological suppression in singly parasitised hosts and to prevent it occurring in super- and multi-parasitised ones. The retarding effects of reduced oxygen tension decrease with the advancing age of the parasitoid larva. Since the oxygen content of the host haemolymph does decrease in the course of parasitism this would be an advantageous adaption to the endoparasite which progressively destroys its host. The minimum measured oxygen uptake of a young parasite larva is about equal to the total dissolved oxygen content of the host's blood at any one time. Thus once the parasite larva has established itself in the host and is respiring oxygen at a rate in excess of the total oxygen content of the haemolymph, its own respiration becomes limited by the rate at which oxygen can diffuse into the blood from the host's tracheae. The progressive lowering of the blood oxygen tension during the development of the parasite suggests that this rate of diffusion may be the critical limiting factor. The hypothesis of asphyxiation is therefore put forward as the mechanism of physiological suppression, by which supernumerary parasitoids are eliminated.

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EFFETS DES COULEURS SUR LE COMPORTEMENT DE DIVERSES RACES DU PUCERON DU POIS, *ACYRTHOSIPHON PISUM* (HARRIS), EN ELEVAGE SUR UN REGIME NUTRITIF DE COMPOSITION CHIMIQUE CONNUE

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Les pucerons sont des insectes délicats qui doivent se nourrir presque continuellement sauf durant la mue ou les migrations. Toute période de jeûne, particulièrement durant les premiers stades larvaires, est susceptible d'influencer la croissance de l'adulte et de diminuer ses chances de survie. C'est là un problème crucial auquel nous avons eu à faire face en voulant élever le puceron du pois, *Acyrthosiphon pisum* (Harris) dans un milieu artificiel et sur un régime nutritif de composition chimique connue. En effet, transférer des larves ou des adultes d'une plante-hôte à un appareil fait de verre, carton, caoutchouc ou Parafilm avec l'espoir qu'elles le colonisent, c'est sans doute exiger du puceron une évolution pour le moins "rapide". Alors, nous nous sommes demandés jusqu'à quel point il était possible de conserver en milieu artificiel certaines caractéristiques physiques de l'habitat du puceron.

En nature, les pucerons recherchent habituellement l'envers d'une feuille et se nourissent dans cette position en présence de lumière solaire atténuée et filtrée par les tissus foliaires. On sait également que les pucerons sont sensibles à la lumière et particulièrement attirés par des surfaces jaunes comme l'ont démontré les nombreux travaux du professeur Moericke. En considération de ces faits, nous avons conçu une petite chambre d'essai très simple et peu dispendieuse pour voir si les pucerons du pois préfèrent certaines couleurs et jusqu'à quel point certaines longueurs d'ondes peuvent favoriser la colonisation des cellules artificielles.

Ainsi, donc, lorsque mises en présence de cellules artificielles éclairées de diverses couleurs, certaines races d'*A. pisum* ont préféré l'orange (605 mμ) ou le jaune (565 mμ) ou dans certains cas les deux couleurs. Si les larves d'*A. pisum* sont élevées sur couleur imposée dans des cellules individuelles, on obtient des effets très variés. Ainsi 96 larves du biotype R1 ont été réparties en groupes de 16 sur chacune des six couleurs déjà mentionnées. Nous avons obtenu une survie totale sur jaune et orange, et mortalité totale sur bleu. Il y eut un survivant dans la cellule blanche et quelques survivants dans les cellules rouges et vertes. Les larves qui survécurent sur cellule verte ont atteint un poids égal à celui des larves élevées sur jaune ou orange. Cela peut indiquer que, même s'il y eût beaucoup de mortalité durant les deux premiers jours, ces larves n'ont pas été rendues agitées par la couleur verte elle-même. Par ailleurs, les larves élevées sous lumière rouge ont eu une croissance de beaucoup diminuée. Il semble que dans ce cas la lumière ait rendu les larves agitées à chaque période quotidienne de 16 heures, ne laissant à celles-ci qu'une nuit de 8 heures pour se nourrir. Il nous semble probable qu'un éclairage rouge quotidien de 24 heures aurait maintenu les larves en état d'agitation permanente provoquant l'inanition à brève échéance.

Les faits nous permettent de conclure, qu'en milieu artificiel, c'est-à-dire, sans être soumis à l'influence d'une plante-hôte, les pucerons du pois sont très sensibles aux couleurs. Les larves et les adultes aptères colonisent les cellules jaunes ou oranges en quelques heures. Les femelles ailées passent au moins 2 jours à s'agiter et à voler avant de répondre au stimulus du jaune ou de l'orange et de coloniser (settling response) une cellule.

Les méthodes décrites laissent entrevoir la possibilité d'étudier dans le détail l'attroupement (the grouping), l'effet de groupe et bien d'autres caractéristiques du comportement des pucerons. Il est à prévoir qu'en modifiant la composition chimique du régime nutritif et en faisant agir la température, la photo-période et la densité des populations que de grands progrès seront réalisés en vue d'élucider plusieurs points encore obscurs du polymorphisme des pucerons.

LONG RANGE MIGRATIONS AND DISPERSAL

ZUR FRAGE DER ABHÄNGIGKEIT DER WANDERRICHTUNG DES TAGFALTERS *AGLAIS URTICAE* L. (NYMPHALIDAE) VON DER LUFTSTRÖMUNG

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Museum Koenig, Bonn, Deutschland

Der Kleine Fuchs (*Aglais urticae* L.) entwickelt im Rheinland/Westdeutschland jährlich 2–3 Generationen, von denen die 1. im Juni/Juli und die 2. ab August die Puppe verlässt. Die ab Oktober schlüpfenden Falter gehören teilweise einer 3. Jahresgeneration an.

In den Jahren 1956-63 wurden zur Erforschung der Wanderungen dieses Falters 45000 im Raum Bonn als Altraupen eingetragene *urticae* nach dem Schlüpfen mit Flügeletiketten markiert und dann dort ausgesetzt. Von 11600 Faltern der 1. Generation wurden 184 zurückgemeldet (Abb. 1 A), darunter nur einer aus mehr als 16 km Entfernung ("Fernfund"). 9600 im August geschlüpfte und ausgesetzte Falter (2. Gen.) ergaben 96 Wiederfunde, davon waren 2 Fernfunde, 18000 in den Jahren 1956-62 ausgesetzte Septemberfalter 219 Rückmeldungen, darunter waren 29 Fernfunde (Abb. 1 B) und 4000 1959-62 ausgesetzte Oktoberfalter 46 Rückmeldungen, darunter war 1 Fernfund. Die Rückmeldungen machen deutlich, dass sich Fernwanderungen bei den Septemberfaltern häufen. Die nachgewiesene Maximalentfernung beträgt 150 km. An den Flügen sind beide Geschlechter beteiligt. An dem Flügverhalten der Septemberfalter ist folgendes bemerkenswert:

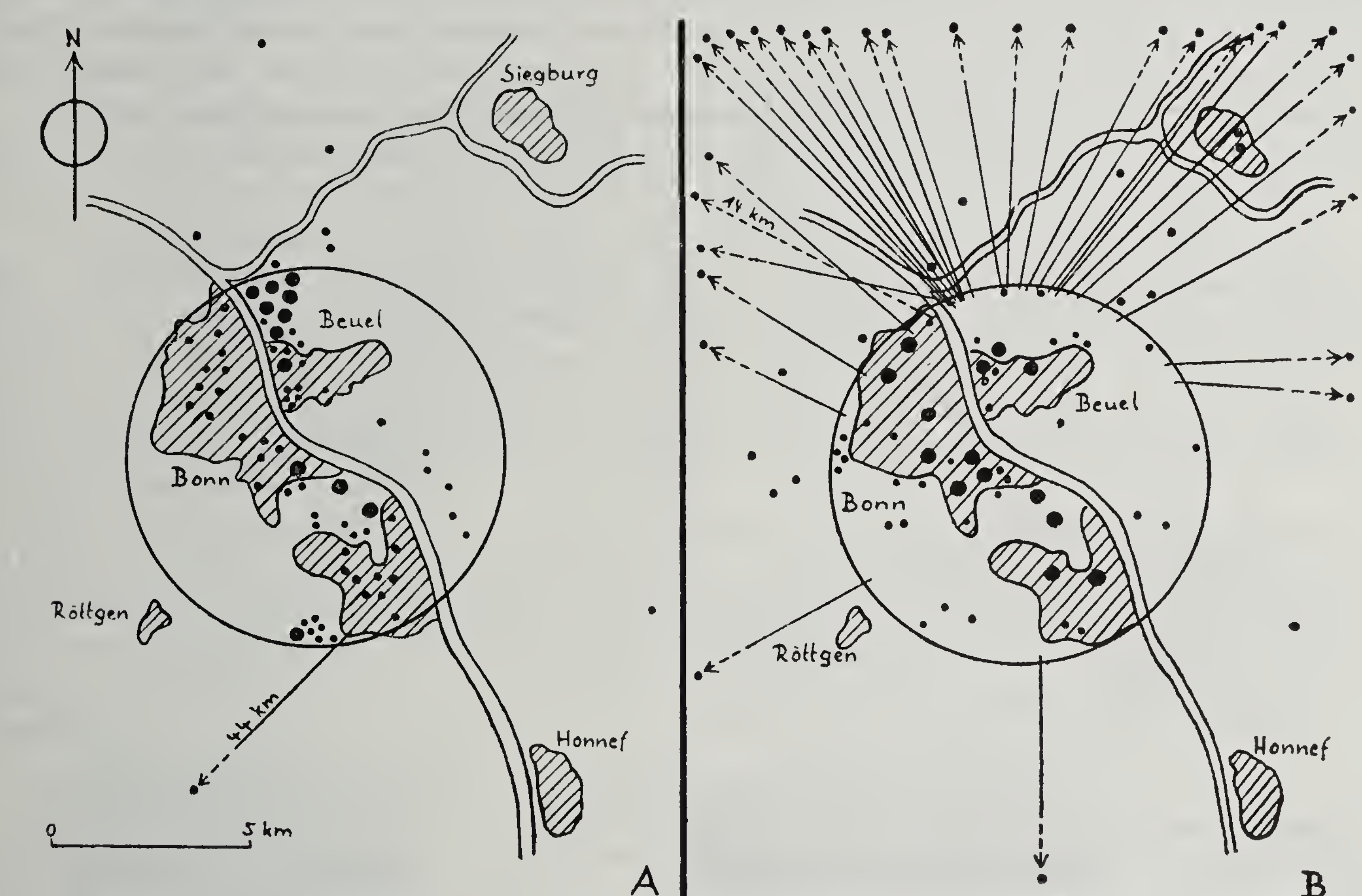

Abb. 1

Wiederfunde im Raum Bonn ausgesetzter urticae Falter

A – Start Juni/Juli 1960-63 (1.Gen.)

B – Start September 1956-62 (2.Gen.)

• – *Einzelfund*

● – *10 Funde*

——--->• – *Fernfund*

1. Nur ein Teil der Population verlässt den heimatlichen Lebensraum, und zwar in den ersten Tagen nach dem Schlüpfen.
2. Die Septemberfalter scheinen die Zugrichtung NW-NE zu bevorzugen.

Die aufgrund mehrerer Fernfunde einen besonderen Aussagewert besitzenden Starts wurden analysiert. Während von den am 8. und 9.9.62 freigelassenen Faltern nur Fernfunde aus nordöstlicher Richtung vorliegen (Abb. 2 A), weisen die am 10.9.62 ausgesetzten auf Abwanderung in nordwestlicher Richtung hin. Ein Vergleich dieser beiden Zugrichtungen mit den Windverhältnissen an den Start- und den ersten Flugtagen danach (Tage mit überdurchschnittlicher Sonnenscheindauer) macht einen Zusammenhang zwischen Flug- und Windrichtung wahrscheinlich. Da Abwanderung vorzugsweise in den Vor- bis Mittagstunden einsetzt, sind die am 10.9.62 um 13 Uhr ausgesetzten Schmetterlinge wahrscheinlich nicht vor dem 14.9. zur Abwanderung gekommen, wiedergefangen wurden die ersten beiden am 15.9. An diesem wie auch am Vortage meldete die im Flugraum gelegene Wetterstation Köln/Wahn südsüdöstliche Luftströmung. Entsprechende Zusammenhänge lassen auch die Starts vom 25.9.62 (Abb. 2 B), an diesem wie auch an den nächsten Wanderflugtagen (26. und 30.9.) lag das Rheinland im Bereich südöstlicher Luftströmung, sowie vom 10.9.61 und 6.9.60 vermuten. Wiederholte Beobachtungen von Mitwind-Abflügen nach Falterstarts sprechen ebenfalls für die Existenz von Mitwind-Migrationen bei *Aglais urticae.*

Die aufgeführten Versuchsergebnisse machen es somit wahrscheinlich, dass vorwiegend Septemberfalter des Kleinen Fuchs zum Ortswechsel grösseren Ausmasses neigen, wobei sie sich von der Luftströmung forttragen lassen. Die in dieser Jahreszeit im Rheinland an charakteristischen Wanderflugtagen vorherrschenden Witterungsverhältnisse—es handelt sich um für diese Jahreszeit milde und sonnige Nachsommertage—führen dazu, dass die Wanderer vorzugsweise nordwestlich bis nordöstlich von ihrem Herkunftsort sesshaft werden. Wenn weitere Untersuchungen diese Befunde bestätigen, so hätten wir hier einen Beweis dafür, dass das Vorliegen einer Vorzugswanderrichtung nicht notwendigerweise die Existenz eines besonderen Orientierungsmechanismus voraussetzt, also endogen gesteuert sein muss.

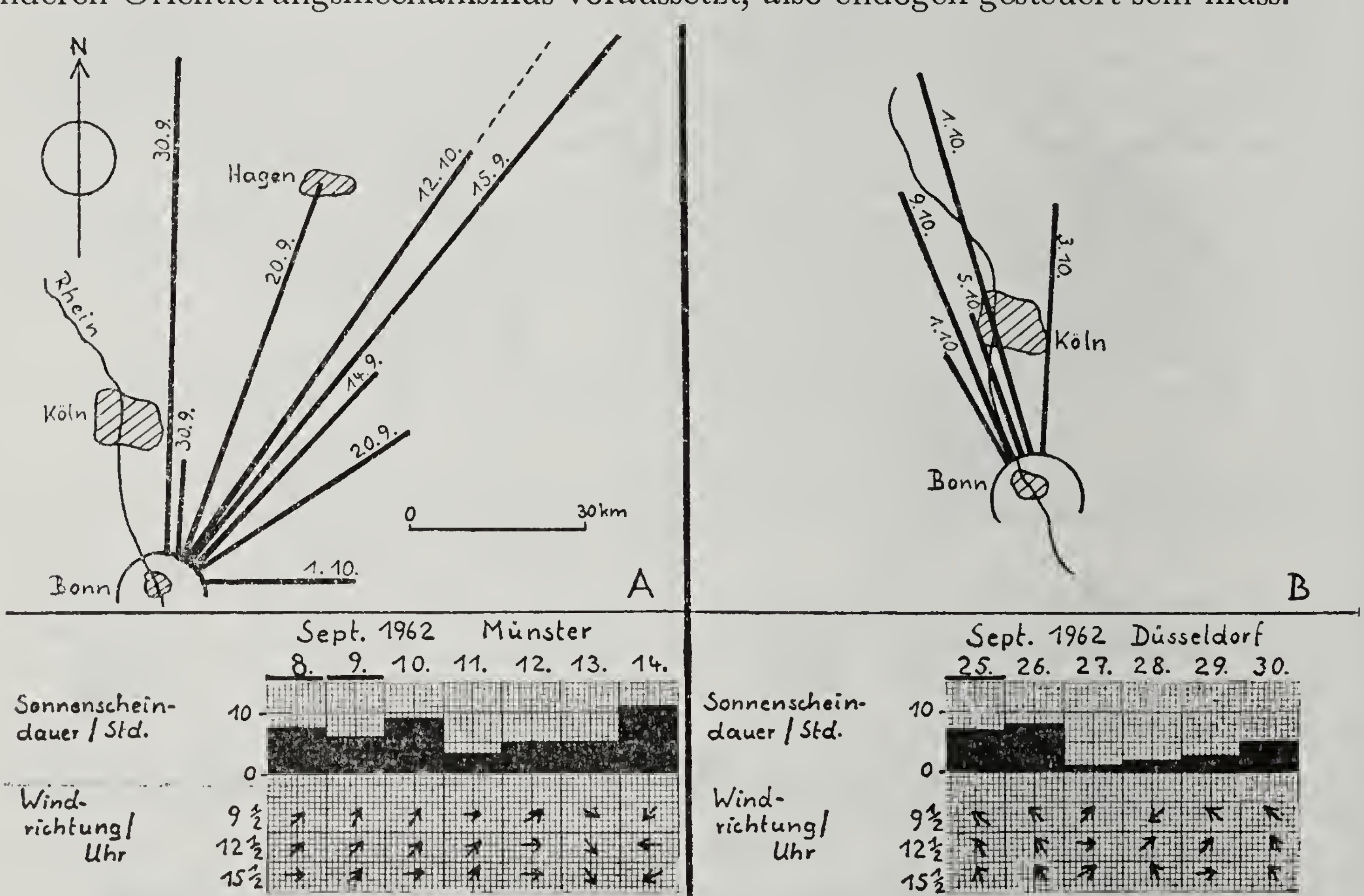

Abb. 2

Vergleich zwischen der Wind-und Wanderrichtung im Raum Bonn ausgesetzter urticae-Falter

Die Wetterdaten sind dem Deutschen Wetterdienst entnommen. Die Windpfeile zeigen in die Richtung, in die der Wind weht. Starttage sind unterstrichen, Wiederfunddaten in den Skizzen angegeben.

DISPERSAL STUDIES ON APHIDIDAE, AGROMYZIDAE, AND CYNIPOIDEA

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This report presents a partial summary of results of the air-borne insect trapping activities aboard ships in the Pacific and Antarctic-Subantarctic areas.

In the initial phase of the trapping program, cubical aluminium frame traps painted with sticky substances (1958, 1959) were used. We next used elongate cone-shaped nylon nets on steel rings of 1 m and 75 cm diameter strung in series using steel cables for lines from mast arms to deck railing of the ships (1960a, 1960b, 1961, 1962a, 1962b, 1963a). Suction traps (1962a, 1963b) were also operated. We consolidated our trapping data and listed 6 families of Hemiptera, 27 families of Diptera, 20 families of Hymenoptera, 3 families of Lepidoptera and 8 other orders of insects, spiders and mites.

Among the many families of trapped insects, we arbitrarily selected three families, Aphididae (Homoptera), Agromyzidae (Diptera) and Cynipoidea (Hymenoptera), for this report. For comparative purposes, arbitrary categories are suggested to group these families into types of fliers. The first type is represented by weak fliers, as winged Aphididae (Johnson, 1955). The second type includes weak-moderate fliers like the Cynipoidea. The third type includes moderate fliers, as Agromyzidae. The fourth and fifth types not treated in this paper, would be the moderate-strong and the strong fliers.

To explain the different trapping results with these families, an attempt is made to show the ability of the insects to fly, the ease by which they become air-borne, and the population ratios in nature where wind-dispersed individuals taken in our trapping program might have become air-borne.

The lateral aphid movement has been studied by Elton (1925), Wadley (1931), Hardy & Milne (1937); and vertical distribution by Berland (1935), Hardy & Milne (1938), Glick (1939), Freeman (1945), Johnson (1957a, 1957b, 1958, 1960) and Taylor (1958).

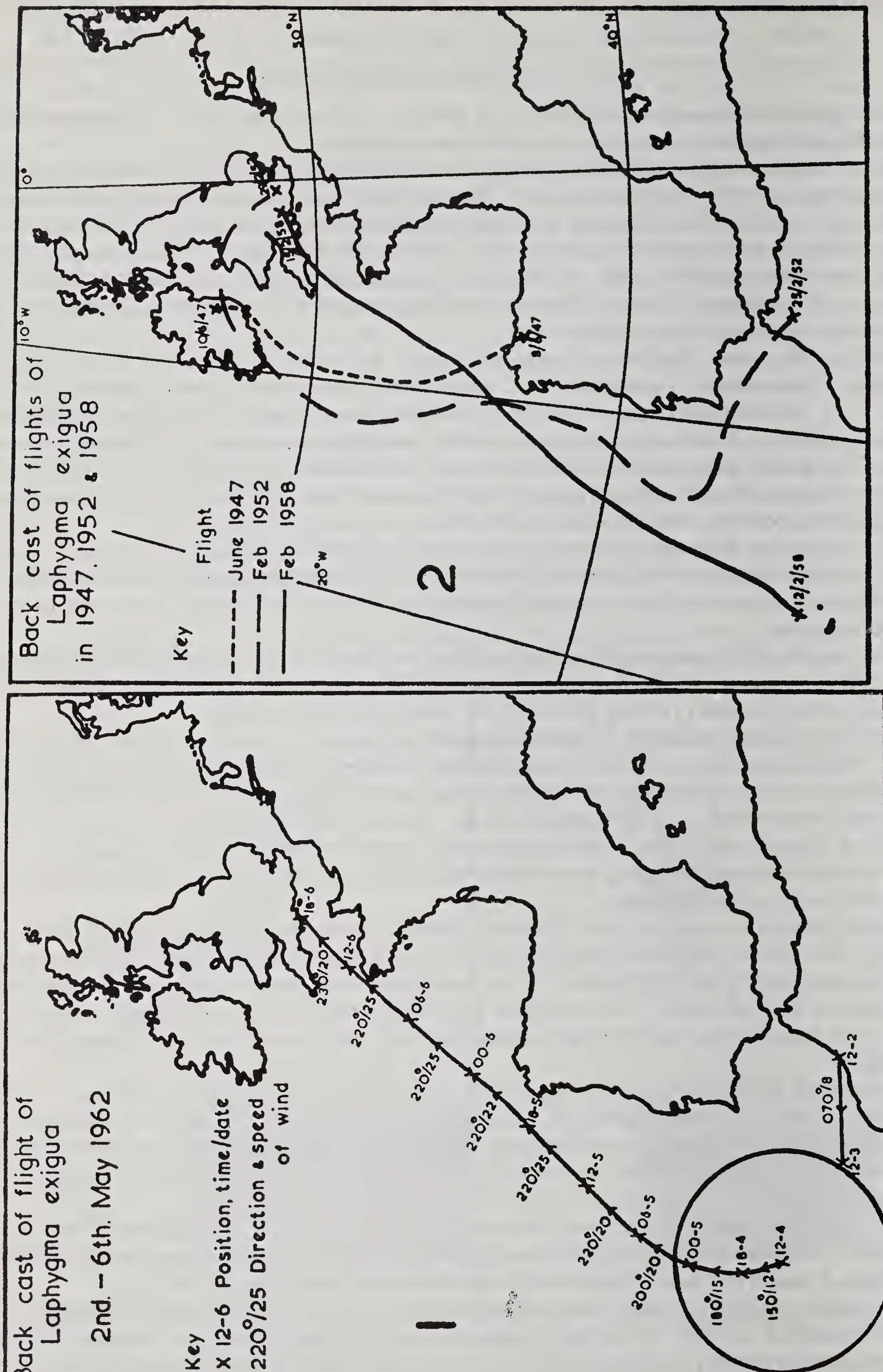
The aerial density of insects depends primarily on terrestrial ecology (Johnson, 1951, 1958, 1960). Preliminary surveys of the three families, Aphididae, Agromyzidae, and Cynipoidea (Eucoilinae) were undertaken on the islands of Iriomote, Ishigaki, and Okinawa of the Ryukyu Archipelago to correlate with our trapping data. Also, in New Zealand, A. D. Lowe, K. A. J. Wise, R. A. Cumber and other workers have made population surveys on these families. The survey methods include sweeping over vegetation with insect nets, use of Malaise traps, light traps, wind nets, and other means.

Aphid population on the three Ryukyu Islands during the month of March 1964 was generally low; clusters of aphids were seen more in the lowlands along stream banks and edges of rice paddies than in the highlands. In the lush lowland vegetation, more Agromyzids were found than in the highlands. The Cynipids were rarely collected by sweeping, but some were taken in the Malaise trap where total number per day's catch was 2 or 3 times more than by sweeping.

Aphids are commonly found on roadside weeds and staple crops in New Zealand. Close and Lamb (1961), Cottier (1953), R. A. Cumber (1959a, 1959b) reported a total of 18 economic species of aphids collected by using sticky substances on traps and insect nets. Thus far, three species of Agromyzids and two species of Cynipids are recorded from the population-ecology studies.

A correlation was made of wind intensity and type of fliers with distances the insects travelled. The weak fliers (Aphididae) were generally found greater distances away from land than those of moderate fliers (Agromyzids) and weak-moderate fliers (Cynipids).

The shortcomings in these dispersal studies are: the trapping data were inadequate for detailed statistical analysis; the season to season insect catches in traps may suggest different interpretations of results; the specimens collected at great distances from land on calm days may be the result of one of many factors, such as aftermath of high wind or storm and fluctuation of air movements in the stratosphere. The ecology of terrestrial insects and the means whereby they become air-borne are to be considered.



Figs. 1 and 2. Back casts of flight of *Laphygma exigua*. (1) May 1962; (2) June 1947, February 1952 and February 1958.

LONG RANGE DISPERSAL OF INSECTS IN RELATION TO SYNOPTIC METEOROLOGY

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Since 1930 records of the occurrence in Great Britain of many species of Lepidoptera believed, or known, to be migrants have been systematically collected. It has been possible to show there is a close relationship between the occurrence of certain species and the synoptic meteorology, in particular the wind (2). Many rely on the wind for dispersal from their winter breeding areas and their arrival in the British Isles depends upon an association of the insects and suitable winds. The distances travelled are often a few hundred miles, and occasionally at least two thousand miles.

In June 1958 the east coast of Scotland and the north-east coast of England were subjected to a massive invasion of *Plutella maculipennis* Curt.; this migratory swarm continued westwards and was recorded in the Atlantic about 300 miles south of Iceland (1 and 4). From information about the times and places of arrival of these moths, the tracks of the winds that carried them could be reconstructed. These tracks led back to an area in N.W. Russia or Finland which are believed to have been the source of the invading *P. maculipennis.*

A smaller number of *Laphygma exigua* Hübn. invaded the south coast of England in May 1962. On this occasion the wind could be traced back to N.W. Africa which appears to be the region from which these moths departed some four days earlier (see fig. 1) (3).

In view of the success in tracking back the 1962 invasion of *L. exigua*, the records for this moth for the years 1947 to 1963 were examined and the wind trajectories constructed. These trajectories, which could be produced for every year, indicated the path flown by the moths and disclosed a seasonal difference in the sources of the migrations. All the early migrations, that is those arriving in Great Britain in February or March, were traced back to N. Africa or Madeira, whereas moths arriving from May onwards were tracked back to the Iberian Peninsular (see fig. 2).

Other species have been treated in a similar manner, and *Nomophila noctuella* Schiff. was tracked to N. Africa, *Utethesia pulchella* L. to Spain, *Hippotion celerio* L. to the Azores and *Itame brunneata* Thun. to Western Germany.

Displacement down wind is responsible for the movement of many species of Lepidoptera long recognised as immigrant into the British Isles.

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SOME FACTORS AFFECTING DISTRIBUTION AND SURVIVAL OF AFRICAN MIGRATORY AND DESERT LOCUSTS

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The invasion area of *Locusta m. migratorioides* R. and F. occupies most of Africa south of the Sahara, and in West and East Africa coincides with that of *Schistocerca gregaria* Forsk., which, however, extends beyond it to northern Africa and south-west Asia.

Field observations on swarm trajectories and comparison of long-range migrations with synoptic situations have shown that *Schistocerca* swarms move with the wind and displace towards, and with, areas of low-level convergence (1). No comparable field observations have been made on *Locusta* swarms, but cartographical analyses of their migrations in West Africa

have shown that they resemble those of *Schistocerca* swarms in following the movements of the Inter-Tropical Convergence Zone. Thus in January-February *Locusta* swarms become concentrated in the belt bordering the Gulf of Guinea where the I.T.C.Z. lies at that season, whereas in spring and summer they gradually spread northwards as far as the most northerly position reached by the Zone in July-August.

It has been shown earlier (2) that solitary *Schistocerca* fly regularly at night, and move to downwind at all but the lightest winds. Similar night flights in solitary *Locusta* were confirmed during recent observations in Eritrea, where it was, moreover, found that marked changes in numbers and morphometrics in a discrete ph. *solitaria* population were associated with the incidence of night winds blowing from the direction of another low-density population situated at a distance of several miles from the first.

There are accordingly strong indications that in both species the geographical and local distributions are likely to be related to winds in which the mobile adults happen to fly. Yet in spite of the considerable overlap in their invasion areas *Schistocerca* and *Locusta* appear to have very different ecological requirements; thus the swarms of the former species breed mainly in areas characterised by sparse and sporadic or strictly seasonal rainfall, ranging from less than 50 to about 500 mm. per annum., while the corresponding range for swarming *Locusta* is from 200-300 to more than 2000 mm. p.a.

Such differences suggest that studies in climatically unstable areas inhabited by both species could provide indication of critical climatic limits. On the Red Sea coast of Eritrea, for example, where mean annual rainfall ranges from 100-200 mm., the temperatures and humidities are high at all seasons, and both *Schistocerca* and *Locusta* find semi-permanent habitats, a season with 310 mm. of rain falling between October and January was marked by a build-up and gregarisation of *Locusta* populations, and by very heavy mortality among the progeny of small *Schistocerca* swarms, caused by *Entomophthora grylli* to which *Locusta* remained immune. It may be suggested that such susceptibility of *Schistocerca* to fungal disease in conditions of sustained high humidities and temperatures could sometimes lead to sharp declines in swarming populations on occasions when exceptionally heavy and protracted rains fall in its tropical breeding areas.

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MIGRATION AND POPULATION CHANGE IN *OSCINELLA FRIT* L. (DIPTERA) ON THE OATCROP

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It has been shown (5, 2) that in the autumn large numbers of frit flies leave the oatfield flying up into the air where they are carried in air currents. The average height of flight on a fine day at mid-day is about 400m; the flies remain airborn for about an hour and may be carried many miles. The question arises as to whether this migratory behaviour is characteristic only of the generation emerging from the panicles or whether the flies also migrate from fields of young or flowering oats.

This problem has been investigated for two years in small fields of oats; a small area was used so that a significant proportion of the total population could be marked. The total daily population was estimated by tents (4) and the emergence of the adults of the tiller generation by the use of large cloth covered cages designed by Calnaido (1). Flight activity was determined by water and suction traps. Large numbers of adult frit flies collected from another field were marked with radio-active phosphorus and sulphur using the method of Lewis and Waloff (3). These flies were released into the field at dusk, when their level of flight activity is normally low; it was hoped in this way to avoid initial large scale dispersal due to disturbance.

In the spring when the flies invade the field the population "build-up" is recorded by

regular tent estimation. On some days the population rises steeply, on others it falls; the fiducial errors of the estimates are such that these differences cannot be claimed to be true. However, if the dispersion pattern of *Oscinella frit* in the oatfield, as determined by the numbers in individual tents, on the days of maximum increase are compared with those on the days of maximum decrease the following differences appear. On the evenings of days of population increase the majority of flies are accumulated on the windward side of the field, on days of population decrease the flies are on the leeward side of the field (wind direction being measured continuously at crop level). The suggestion that the flies are blown in and out of the crop is supported by the catches in water traps around the field.

This indication that flies leave the field is strengthened by the rapid fall off in the number of radio-isotope marked flies, although in the early spring it is difficult to mark and sample a significant number.

At the time when the oats are coming into flower and the tiller generation adults are emerging it is found that the cumulative total emerging in the field is more than twice the actual population. This shows that at least half the population must migrate; that the proportion of migrants is far higher is shown by the failure to recapture any marked flies after the eighth day after release, even when nearly a quarter of the population had been marked. Samples of the marked flies retained in the laboratory lived for 6-9 weeks and the marks were detectable for at least 10 days. It is concluded therefore that *Oscinella frit* is a migratory insect at all seasons and that the individual composition of the population of an oatfield is continually changing.

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RELATIONSHIPS BETWEEN SPECIES IN THE SAME HABITAT: INSECT COMMUNITIES

NATURAL REGULATION IN FIELD POPULATIONS OF TWO CLOSELY RELATED CO-EXISTING SPECIES

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Two closely related psocid species, *Mesopsocus immunis* and *M. unipunctatus* live together on the same trees and feed on the same food at the same time in larch plantations over a wide area in Yorkshire below 800 feet altitude. In a larch plantation at Harrogate they occur in roughly equal numbers and are very abundant. They feed on the intimate mixture of *Pleurococcus* and fungal spores present on the trunk and branches. The density distributions of nymphs along larch branches are very similar so that these two species are feeding at the same place. Their phenology is almost identical. The overwintering eggs of both species hatch at the same time in early spring; nymphs pass through six instars and the adults emerge, lay eggs and die out over the same period in July in both species. Both are attacked by the same egg parasite—the mymarid *Alaptus fusculus* and by a braconid, *Euphorus* sp., which attacks the 5-6th instar nymphs of both species. The important predators—a larval lacewing and various birds—appear to attack both species indiscriminately since the survivorship curves, although varying in shape from year to year, are very similar in both species in any one year. The biomass of each *Mesopsocus* population reaches peak value in the same week and this coincides with the period of maximum reduction of *Pleurococcus* on the twigs. Four other psocids and one collembolan feed on the remaining *Pleurococcus* later in the summer.

Problems of the existence and intensity of interspecific competition for food or other resource and of the stability of their coexistence in nature can most profitably be assessed only within the wider context, that of the regulation of their numbers.

Studies of the dispersion patterns of the two species over 11 kinds of tree in a mixed woodland and also within a larch and a pine plantation give no indication of mutual exclusion and suggest that no strong competitive interaction is occurring. The two species are evidently coexisting in a stable way. The very similar changes in both species in their numbers from year to year over a six year period confirms this conclusion and indicates also that the two species are reacting to their total environment in a remarkably similar way.

Since eggs, as well as nymphs and adults, can be recognised and sampled, a quantitative study of the life cycle over 4 years has been carried out. Mortality factors have been assessed and life tables drawn up for the two *Mesopsocus* species and for the mymarid parasite. Regression analysis reveals a regulatory process occurring at the beginning of adult life just prior to egg laying. When densities are high females emigrate from the sample zone and immigration occurs when densities are low. The sample zone is the favoured oviposition region for both species so that, with respect to the populations within this sampled portion of the habitat, intraspecific competition for oviposition sites appears to regulate the numbers of each species, but the lack of significant relationship between numbers of the two species at this period suggests that interspecific competition for oviposition site does not occur. There is a modal difference between the species in the dispersion patterns of their eggs along a larch branch and in the exact sites chosen for oviposition.

A quantitative model has been set up incorporating (1) survivorship values for certain stages in the life cycle, (2) the Nicholsonian host-parasite equation relating the mymarid and braconid to their two hosts and (3) the regression equations describing the numerical changes occurring at the pre-oviposition period and those involved when the eggs are laid. This model describes a regulated system in which all four species reach equilibrium values within or close to the ranges of abundance observed in the field.

FACTORS DETERMINING THE DISTRIBUTION OF THE TWO RELATED STINK BUGS, *NEZARA VIRIDULA* L. AND *N. ANTENNATA* SCOTT

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Field surveys have been carried out for the last five years at Asso where *N. viridula* is greatly predominant and at Kogawa where both it and *N. antennata* are co-existing, to determine the mechanism of distribution of the two species.

Host plants and natural enemies were common to both species at Kogawa, and no difference in the percentage parasitism was found between the two. However, there are at least two biological differences between the two species, (1) *viridula* has three whilst *antennata* has two generations a year, and (2) the former lays two to three times more eggs than the latter. Therefore, if the survival rate of both species were the same, *viridula* would predominate in number as time elapses. But this assumption was not found to be valid at Kogawa, because *viridula* was more susceptible to winter conditions than *antennata*. For example, in the spring of 1962 the percentage of *viridula* was 63·8%, however, following the severe winter of 1963 the percentage of hibernated *viridula* was only 4·2% and that of *antennata* 95·8%.

Natural inter-specific matings between *viridula* and *antennata* were observed in the field. A total of 54 mating pairs of *Nezara* were observed in May, 1964 at Kogawa. Out of these 54 pairs, 11 were *viridula* female and *antennata* male. The reverse mating between *antennata* female and *viridula* male was rarely observed. This was also confirmed by the mating experiments in the laboratory, inter-specific mating between these two species invariably resulted in a deposition of unfertilized eggs. The mating between *viridula* female and *antennata* male apparently occurs because *viridula* matures sexually earlier than *antennata* and also because males of both species mature earlier than females. Such inter-specific matings of either combination may have a deleterious effect upon the persistence of either species.

Recent increases of *viridula* in southern Japan were caused by the early planting of paddy of which heading time coincides with the emergence period of its first brood, but this was not the case in *antennata*. In addition, the preference of *viridula* for rice and its high reproductivity would have contributed in making Asso a single population area of *viridula* during the last ten years. A few cases of mating of *antennata* observed at Asso in 1961-2 were invariably inter-specific ones which prevent *antennata* from producing offspring. On the contrary, as at Kogawa where the area of early paddy is negligible, both can co-exist almost permanently unless the cultural custom changes or severe climatic conditions eliminate either species. The areas of single population of *antennata* have been established largely due to the climatic conditions prevailing in those areas, and the northern limit of the sympatric area is primarily determined by the climatic conditions in a single year or in a few consecutive years.

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THE INTERACTION OF TWO SPREADING POPULATIONS

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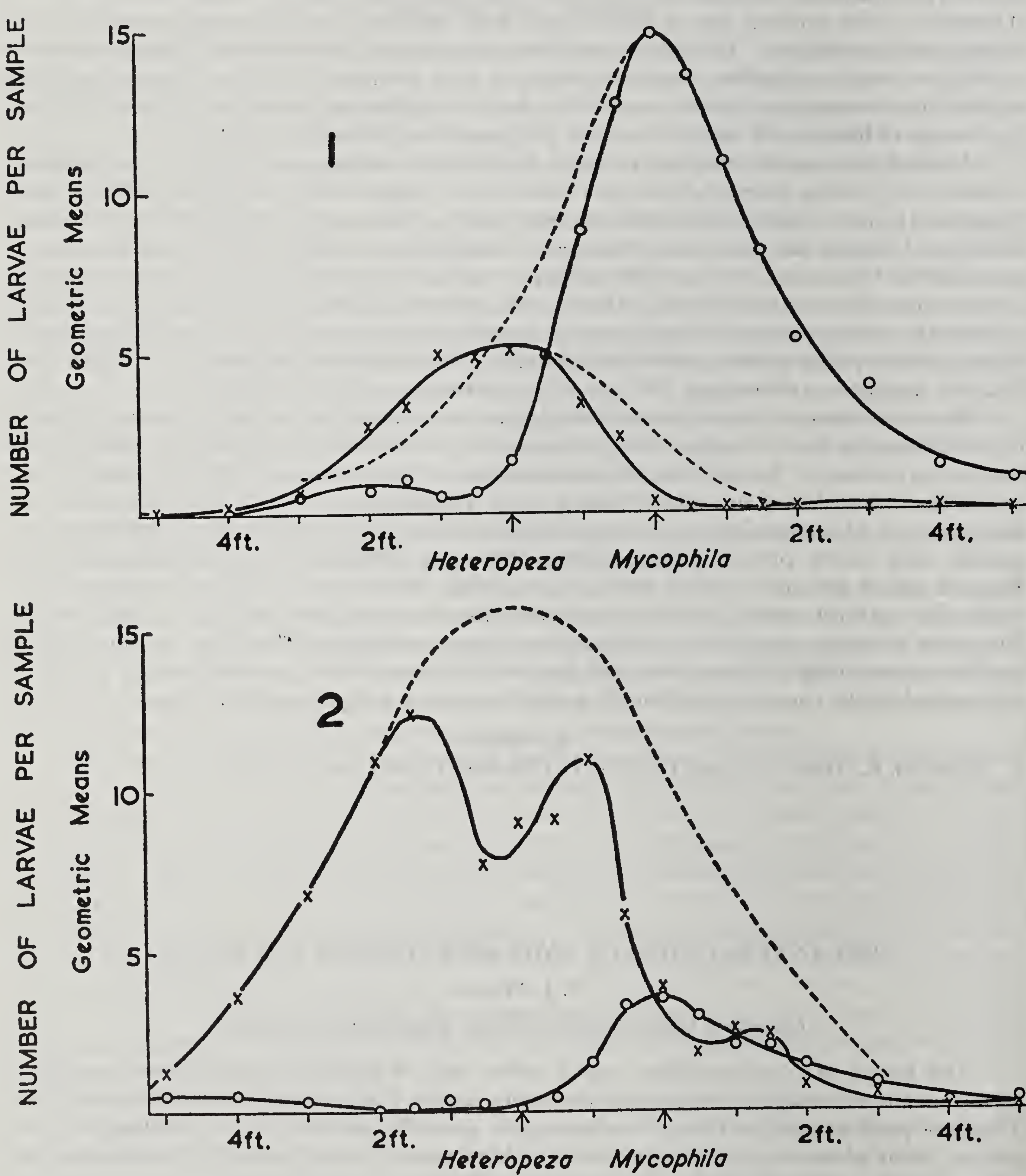
The larvae of Cecidomyiidae, which infest beds of cultivated mushrooms, provide a useful means of studying population dynamics under fairly closely controlled conditions. They are paedogenetic and thus development is normally confined to larvae alone, the dispersive adult phase occurring infrequently. Mushroom compost provides a uniform, continuous medium through which larvae can move freely.

In order to study the interaction of spreading and competing populations, two readily distinguishable species were used: *Heteropeza pygmaea* Winnertz, which has white larvae, and

Mycophila speyeri (Barnes), which has orange larvae. 100 larvae of each species were placed in two parallel rows, two feet apart, across the centre of a mushroom bed 12 ft. long and 4 ft. wide. On three subsequent dates, core samples were taken on transects along the bed, at six inch intervals. In all, four transects were sampled on each date, from two such beds.

At the first sampling, six weeks after introduction, *M. speyeri* had reached its highest recorded population density at its centre of spread, *H. pygmaea* having reached only a third of the density. Each species exhibited an approximately normal spatial distribution about its introduction point, except that where the populations intermingled, each was noticeably impeded in its spread by the other, resulting in a marked asymmetry of the two distribution curves.

Three weeks later the *M. speyeri* population had not spread or multiplied further, but



Figs. 1 and 2. Interaction of spreading populations of *Heteropeza pygmaea* and *Mycophila speyeri* after (1) 6 weeks and (2) 11 weeks.

H. pygmaea had almost achieved the same central density and had an even wider spread. The asymmetry of the distribution curves still remained.

After two more weeks the *H. pygmaea* population was still increasing exponentially, but its distribution no longer approximated to the normal. A deep central depression indicated that the mycelium had been adversely affected by the high population, and a second depression coincided with the population centre of *M. speyeri*. Only a small remnant of the *M. speyeri* population persisted, still distributed asymmetrically about its point of introduction.

The asymmetry in the first two samples can be described as a simple reduction in numbers of one species equal to a proportion of the population density of the other. In the final sample, deviations from the normal can be related to the combined high densities of both species at an earlier date.

THE DISTRIBUTION AND SURVIVAL OF TWO CERCOPIDAE (HOMOPTERA) NEAR TO THE EDGE OF THEIR RANGE IN NORTHERN ENGLAND

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The distribution and survival of two cercopid species *Neophilaenus lineatus* (L.) and *N. exclamationis* (Thun.) were studied on the Moor House National Nature Reserve at 1,800 feet altitude on the Pennine hills where both species are near to the edge of their ranges. Comparative information on *N. lineatus* in a lowland population at Wytham Hill, Berkshire, is also presented and on *Conomelus anceps* (Germar) (Delphacidae) and *Macrosteles alpinus* (Zett) (Cicadellidae) at Moor House.

N. lineatus was studied on an area dominated by *Juncus squarrosus* and *Festuca ovina* and also on an almost pure stand of *Nardus stricta*. *C. anceps* and *M. alpinus* also occurred in the *Juncus* area. *N. exclamationis* was restricted to *Festuca* spp. on an area of limestone grassland nearby. Its distribution did not overlap that of *N. lineatus*.

N. lineatus completed its life cycle on *Nardus stricta* and *N. exclamationis* did likewise on *Festuca* spp. *N. lineatus* on the *Juncus* site, however, changed hosts from *Festuca ovina* to *Juncus squarrosus* in instar three or four. Movements of *N. lineatus* after moulting were demonstrated on the *Nardus* and *Juncus* sites by a study of the changes in their distribution as measured by Blackman's coefficient of dispersion. *N. exclamationis* nymphs showed no such moves.

The nymphal mortality was in part related to these movements, survival of *N. lineatus* being least on the *Juncus* site at the time of change of host plants, and greatest in *N. exclamationis* where no detectable moves occurred.

The populations of both cercopids were about five times as dense in 1961 as in 1962 but overall nymphal mortality was independent of density and was approximately three times as great as in *N. lineatus* in a lowland locality at Wytham (85% and 30% respectively).

Adults of *N. lineatus* and *N. exclamationis* at Moor House suffered chance catastrophic mortality before oviposition, due to unfavourable climate. *N. lineatus* became temporarily extinct above 2,200 feet in 1962 (it occurred up to 2,700 feet in 1961). This was because the life cycle was not completed before the autumn frosts.

Egg mortality of *N. lineatus* was a maximum of 25% in 1961-62 and a minimum of 25% in 1962-63.

There was no evidence of density dependent mortality at any stage in the life cycles of *N. lineatus* or *N. exclamationis* at Moor House and the same was true of a delphacid, *Conomelus anceps* which was also near to the edge of its range. *Macrosteles alpinus*, a sub-arctic cicadellid (presumably living at nearer optimum conditions at Moor House) showed evidence of density dependent mortality in the nymphal stages.

At the edge of the range of a species chance plays an increasing role in the population dynamics of insect populations, and local extinctions are likely occurrences. Even under the rigorous conditions at Moor House, the population of *N. lineatus* would have maintained a fairly steady state were it not for the chance catastrophic mortality of adults. Thus it seems reasonable to assume that a population of *N. lineatus* occurring where climate and other habitat features are optimal would expand rapidly if some density related factors did not operate. This situation is at present being studied at Wytham Hill.

THE COEXISTENCE OF THREE SPECIES OF *ORTHOTYLUS* (HETEROPTERA, MIRIDAE)

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Scotch broom, *Sarothamnus scoparius* (L.) Wimmer is a native shrub. In southern England it supports a large insect fauna which includes 35 species confined to it. Amongst these are five species of Miridae—*Heterocordylus tibialis*, *Asciodema obsoletum* and three closely related species—*Orthotylus adenocarpi*, *O. virescens* and *O. concolor*. Their coexistence may be facilitated by a number of factors and although there is a considerable overlap in the times of their occurrence, the periods of their maximum abundance are spread out in time. *O. adenocarpi* is the earliest and *O. concolor* the latest species to hatch. Eclosion spreads over three months and this is reflected in their geographical distribution. *O. adenocarpi* has a wide southern Atlantic range (Southwood, 1957), whereas *O. virescens* extends into southern Europe, Asia Minor and North Africa. The distribution of *O. concolor* is less well documented but it is probably similar to that of *O. virescens*.

The three species differ in details of their behaviour. They show a tendency to oviposit in somewhat different parts of the broom shoots and while *O. virescens* and *O. concolor* lay in one year old stems, *O. adenocarpi* mostly lays in two year old ones. There are also differences in their feeding habits (Dempster, 1960) which may be related to the differences in the lengths of rostrum: *O. adenocarpi* with the longest rostrum is a more predacious species than *O. virescens* with the shortest rostrum. Further there is some evidence that large numbers of adults emigrate from overcrowded conditions and that *O. virescens* and *O. concolor* are capable of dispersing more rapidly over a wide area than the other broom Miridae (Waloff and Bakker, 1963).

The abundance of broom mirids is partly controlled by parasites of eggs and nymphs. Three *Leiophron* spp. (Euphorinae, Braconidae) lay eggs in the first instar nymphs of the five mirid species. There appears to be no strict host specificity, but the degree of parasitism is related to the times of emergence of parasites and of hatching of mirids. (Professor O. W. Richards is now working on the taxonomy of these Braconids).

Both *O. concolor* and *O. virescens* have been introduced together with broom into California: *O. concolor* is the least abundant of broom mirids in England, but in California it reaches a degree of abundance which exceeds that of all the five species in southern England. In the foothills of the Sierras it is the only broom mirid and I did not find any parasitised nymphs. In British Columbia *Asciodema* is found with the two above species, but there it is *O. virescens* which occurs in greatest numbers. Nymphs are parasitised, probably by a *Leiophron* sp., but extremely lightly. In all probability even in the absence of *O. adenocarpi* and some nymphal parasites there is competition between the other two broom species of *Orthotylus*, but simultaneously the climatic background affects their abundance as a seesaw.

DIE BESIEDLUNG VON NEULAND AN DER DEUTSCHEN NORDSEEKÜSTE DURCH PROCTOTRUPIDEN (HYMENOPTERA)

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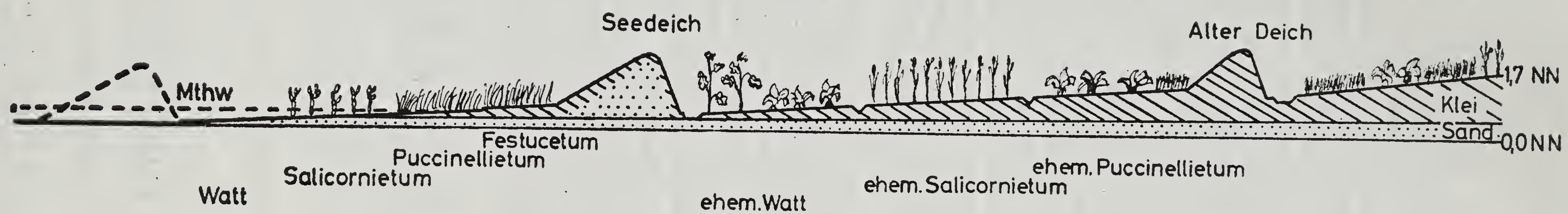
Der Bau von Deichen zur Gewinnung von Neuland aus dem Meer kann als Freilandexperiment zum Studium der Sukzession vom vegetationslosen Watt über Salzwiesen zur reifen Marsch ausgewertet werden. Heydemann (1) hat erstmalig diese Entwicklung an Hand des Epigaion untersucht. Im Folgenden soll die Besiedlung des Neulandes durch die Käfer parasitierende Terebrantia-Familie der Proctotrupidae dargestellt werden (vgl. 2).

Material und Methode. Das Material (4439 Individuen aus 13 Arten) verdanke ich der Zusammenarbeit mit Herrn Dr. B. Heydemann, Universität Kiel.

VORLAND (Bongsiel 1958/59)	JUNGER KOOG (Lübke-Koog 1957/59)	ALTER KOOG (Wiedingharder N. Koog 1957/59)
	Proctotrupes gravidator	P. gravidator
	Proctotrupes gladiator	P. gladiator
	Codrus brevicornis	C. brevicornis
C. ligatus	Codrus ligatus	C. ligatus
	Codrus microcerus	C. microcerus
	Codrus ater	C. ater
C. gracilis	Codrus gracilis	C. gracilis
C. confusus	Codrus confusus	C. confusus
	Codrus curtigena	C. curtigena
P. calcar	Phaenoserphus calcar	P. calcar
	Phaenoserphus viator	P. viator
	Phaenoserphus pallipes	
	Paracodrus apterogynus	P. apterogynus



Untersuchungsgebiete. Die Untersuchungen wurden an der schleswig-holsteinischen Nordseeküste nahe der deutsch-dänischen Grenze durchgeführt:

1. Bongsiel: während der Untersuchungen 1958/59 eingedeicht,
2. Lübke-Koog: 1954 eingedeicht,
3. Wiedingharder Neuer Koog: 1927 eingedeicht.

Die Proctotrupiden-Sukzession

Deichvorland. Das erste von Proctotrupiden besiedelte Areal außerhalb des schützenden Deiches sind die Salzwiesen des Puccinellietum und Festucetum. Vor allem das Puccinellietum wird in seinen unteren Bereichen noch regelmäßig überflutet, während das Festucetum nur von besonders hohen Fluten erreicht wird. Bereits im Puccinellietum sind drei Proctotrupiden-Arten in geringer Abundanz anzutreffen (vgl. Abb. 1). Die vierte tritt im Festucetum hinzu. Alle vier Arten sind in ganz Europa häufig und weit verbreitet. Die Aufzucht von *Codrus ligatus* und *Phaenoserphus calcar* aus dem küstengebundenen halobionten Staphyliniden *Quedius simplicifrons* FRM. (Col.) beweist ihre Indigenität in diesem Lebensraum.

Jungkoog. Wenn das Vorland infolge anhaltender Sedimentation eine genügende Breite erlangt hat, wird es eingedeicht und so vor Überflutungen geschützt. Als Effekt dieser Maßnahme zeigen *C. ligatus* und *P. calcar* eine geringe Abundanzsteigerung. Erst nach der Kultivierung im 2. bis 5. Jahr nach der Eindeichung gewinnt die Proctotrupiden-Synusie mit 13 Arten ihre reichste Entfaltung (vgl. Abb. 1). Der Anstieg der Artenzahl erfolgt ein bis zwei Jahre nach dem bei Käfern festgestellten Zeitpunkt. Die Abundanz der vier Arten der Salzwiesen und des unkultivierten Jungkooges steigt um 100%.

Mit Feldern des Binnenlandes von Schleswig-Holstein und des Rheinlandes bei Köln besitzt der unter Kultur genommene Jungkoog 80% gemeinsame Arten. Als Folge der Kultivierung wird also innerhalb von drei Jahren eine typische Agrar-Synusie der Proctotrupiden ausgebildet.

Alter Koog. Im alten Koog mit vorherrschender Weidewirtschaft bleibt die Artenzahl erhalten, während die durchschnittliche Abundanz der einzelnen Arten korrespodierend mit der der epigäischen Käfer absinkt.

Sukzessionsbedingungen. Für den Ablauf dieser Sukzession scheinen folgende drei Faktoren besonders bedeutsam zu sein:

(*a*) *Wirte.* Da die Proctotrupiden, soweit bekannt, oligophag sind, können sie neue Areale besiedeln, wenn Wirte geeigneter Größe und Phänologie vorhanden sind.

(*b*) *Luftfeuchtigkeit.* In den Untersuchungsbebieten wird hohe Luftfeuchtigkeit gewährleistet durch die Meeresnähe sowie durch die hohe Wasserkapazität und das große Wasserhaltevermögen des tonreichen Marschbodens.

(*c*) *Windschutz.* Die Proctotrupiden sind sehr windempfindlich. Sie fliegen daher zu 80-90% im Bereich bis 50 cm über der Bodenoberfläche, wo ihnen die Vegetation Schutz vor Verdriftung in den windreichen Küstenbiotopen bietet.

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FALLENFANG UND SYNÖKOLOGIE (COL. SILPHIDAE ET CARABIDAE)

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Für diesen Beitrag konnte ich insgesamt 30,305 Imagines von 8 *Necrophorus*-Arten und 40,123 Individuen von einigen Feldcarabiden-Arten synökologisch auswerten.

Zur Synökologie der Totengräber. Der Aufstieg der Fangquoten von *Necrophorus sepultor*

Charp. und *Necrophorus interruptus* Steph. (Larvenüberwinterer = L-Arten) war in allen 9 Untersuchungsräumen im zweiten Jahre ausgeprägt, wogegen die Fangzifferschwankungen von *N. vespillo* (L.), *N. germanicus* L., *N. antennatus* Reitt., *N. vestigator* Herschel und *N. humator* F. (Imagoüberwinterer = I-Arten) im positiven und negativen Sinne nicht so auffallend waren. Für den Gradationsfaktor der Larvenüberwinterer halte ich den infolge Fallenfang dezimierten I-Artenbestand, welcher den Wettbewerb um Aas zu gunsten der L-Arten herabsetzt. Sind also einmal die I-Arten im ersten Untersuchungsjahre auf ganz bestimmten Lebensstätten durch die beköderten Fallen dezimiert—das heisst—ist durch den Fallenfang eine beträchtliche Anzahl der Imagoüberwinterer aus der Konkurrenz mit den Larvenüberwinterern im Sommer und Herbst des ersten Fangjahres ausgeschaltet, so steigt im zweiten Untersuchungsjahre die Besatzdichte der L-Arten auffallend.

Die Analyse der Sammelproben in Bezug zu den Saisonaspekten und Artenspektren zeigt, dass man einen scharfen Wettbewerb um Aas besonders zwishen den Imagines von *N. vespillo* und beiden Larvenüberwinterern erwarten kann. Die körperlich schwächste Art *N. interruptus* unterliegt in diesen Zusammentreffen am ehesten. Ausserdem wird die Abundanz dieser Art von *N. sepultor* auf gemeinsamen Lebensstätten ersichtlich herabgesetzt. Stellenweise setzt sich stark die Abundanz von *N. germanicus* durch. Diese konkurrenzkräftigste Art steht an der Spitze der biologischen Rangordnung der behandeltetn *Necrophorus*-Arten, weil sie ihnen von vornherein überlegen ist. Zu den Konkurrenten der L-Arten gehört auch die Waldart *N. humator,* wobei die Bewegungsaktivität von *N. antennatus* und *N. vestigator* zur Vermehrungszeit der Larvenüberwinterer nicht mehr bedeutsam zu sein scheint.

Zur Synokölogie der Laufkäfer. Insgesamt konnte ich in den Sammelproben aus 7 Rübenschlägen von Haná 60 Carabiden-Arten feststellen; die meisten aber in so geringen Fangzahlen, dass sie für die synökologische Auswertung nicht in Betracht kamen (Material aus 5 beköderten Fallen = FM, Material aus 5 köderlosen Fallen = F).

Die von Standort zu Standort und innerhalb des Jahres stark schwankenden Restwerte (FM-F) mancher Carabidenarten standen im engen Zusammenhang mit Aktivitätsdichte und Abundanz der häufigsten Art *Pterostichus vulgaris* L. Wo zum Beispiel auf den Versuchsschlägen *P. vulgaris* nur in geringer Individuendichte vorkam, war die Imaginesausbeute der Art *Calathus fuscipes* Goez. aus FM um mehr als 50% höher wie die aus F. Wo aber im Gegenteil die ersterwähnte Art auf einem Schlage massenhaft auftrat, erreichten die Restwerte (FM-F) der erbeuteten Imagines von *C. fuscipes* summarisch kaum 7%.

Es muss damit gerechnet werden, dass die räuberisch lebenden Laufkäfer in manchen Tages- und Nachtstunden rings um den Fallen mit Fleischköder erheblich grössere Individuendichte entwickeln als die, welche Formalinfallen ohne Köder belaufen. Vorläufige direkte Feldbeobachtung zeigte, dass etwa ein Drittel der Laufkäfer, welche sich in der unmittelbaren Nähe einer Falle bewegen, auch in der Falle endet; hie und da nicht ohne Zusammenstösse Möglicherweise infolge Konkurrenzdruckes hinsichtlich der totalen Überlappung oder der wenigsten teilweisen Beschneidung der Aktivitätsspannen von *P. vulgaris* einerseits und von *C. fuscipes, Harpalus pubescens* Müll., *Trechus quadristriatus* Schrnk., *Bembidion lampros* Hrbst. und *Carabus scheidleri* Pnz. andererseits, zeigten sich die Restwerte (FM-F) der letztgennanten Arten auf solchen Standorten gering, wo *P. vulgaris* massenhaft auftrat. Das Entkommen mancher erbeuteten Laufkäfer (besonders der kleinen Individuen von *B. lampros* und *T. quadristriatus*) aus den Köderfallen in den letzten Tagen einer ausgiebigen Fangperiode darf man in Gegenteil zum Gesagten nicht ausschliessen.

Weiteres Beweismaterial und besonders eine gründliche experimentelle Überprüfung der vorgelegten Befunde sind wünscheswert.

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SOME FEATURES OF THE DIPTEROUS FAUNA OF SMALL MAMMAL BURROWS

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During the years 1959-1963 the author has studied the dipterous fauna in the burrows of small rodents in various parts of Finland. In three localities funnel and Barber traps were used for this purpose during most of the warm season (1). Rearing tests were also made. In addition, a collection of Diptera from *Talpa* burrows in South Sweden (leg. G. Israelson) was studied.

The material obtained by trapping was comparatively rich in species not only in Southern Finland but also in Lapland. A high proportion (60-75%) of the species were xenocoenic and the tychocoenic element included many more or less ubiquitous species. The species regarded as eucoenic will be specially considered in four selected cases below:

(1) Burrows of moles and mice (*Sylvaemus* sp. ?, secondary inhabitants). South Sweden (lat. 56°10′ N). Diptera trapped even in the winter. Eucoenic: *Eccoptomera microps* Meig. (Helomyzidae), *Leptocera talparum* Rich. (Sphaeroceridae), *L. pseudonivalis* Duda. About 20 tychocoenic spp.

(2) Burrows of the Brown Rat. South Finland (lat. 60°10′ N). Winter temperature at 0°C or a few degrees below. Eucoenic: *Leptocera talparum* Rich. About 30 tychocoenic spp.

(3) Vole burrows, about 10 cm deep. Central Finland (lat. 63°25′ N). June-August +8°–+18°C, slow fluctuations, winter temperature as in case 2. Eucoenic: *Leptocera talparum.* About 35 tychocoenic spp.

(4) Vole and lemming burrows. Lapland (lat. 69°44′ N). In vole burrows in moss June-August +1°–+16°, great daily fluctuations. In lemming burrows (25 cm deep) +1°–+3° during the warm season. No eucoenic species, about 20 tychocoenic spp.

The eucoenic species and most of the tychocoenic ones feed as larvae mainly on animal excrement and are in this way dependent on the present of the host. *Eccoptomera microps* and *Leptocera pseudonivalis* prefer mole burrows but they continue to occupy the burrows when these are secondarily inhabited by rodents. The saprophagous eucoenic species obviously prefer certain types of burrows but are much less dependent on the species of host mammal.

The four cases above represent different microclimates, the 4th being the most different and extreme. In cases 3 and 4 the yearly fluctuations of the populations of host species are remarkable. Large groups of burrows in a locality may be abandoned for years. This causes instability of these rodent burrows as a biocoenosis. In Lapland the microclimate is probably too extreme even for *Leptocera talparum* and the instability of the biocoenosis has apparently prevented specialisation of arctic species for this niche. It can also be assumed that the speciation of the eucoenic element has taken place in the burrows of those mammals which show less strong population fluctuations (moles, rats and others). A number of the tychocoenic species are adapted for a saprophagous life in hypogeous cavities. To this group belong *Bradysia bicolor* Meig. (Sciaridae), *Anevrina thoracica* Meig. (Phoridae), *Eccoptomera ornata* Loew and *E. longiseta* Meig. (Helomyzidae), *Leptocera bequaerti* Vill. and *L. racovitzai* Bezzi.

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OBSERVATIONS ON DIPTERA IN COW DUNG AND THEIR PARASITES

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Observations were made on *Musca autumnalis* Degeer and some Diptera associated with it in cattle droppings. The other flies were *Orthellia caesarion* (Meigen), *Sarcophaga latisetosa* Parker, *S. l'hermineri* R. D., and *S. querula* Walker. The period of fly breeding in cattle dung was from May until September, although some *Sarcophaga* spp. larvae were active in October.

The population counts were based on larval collections from the cattle droppings. *M. autumnalis* increased in numbers from May until August and then decreased in September, when the adults went into hibernation. No maggots of this fly were taken in October. *Orthellia* increased slowly until September when 60% of the larvae were collected. The *Sarcophaga* spp. increased gradually throughout the summer. The larval population reached a near maximum by July and remained fairly uniform throughout August and September. Even though the population decreased during the latter part of September some maggots could be found in October.

The parasites attacking the maggots and reared from the puparia were *Aphaereta pallipes* (Say), *Eucoila* sp. and *Xyalophora quinquelineata* Say. The braconid, *A. pallipes*, was encountered quite commonly. This attacked *M. autumnalis* and *Sarcophaga* spp. at a rate of about 12% and *Orthellia* at about 9% throughout 1960, 1961 and 1963. However, during the summer of 1962, a cool wet summer, *Musca* and *Sarcophaga* were attacked at rates of 32% and 20% respectively. Two other flies *Paregle cinerella* Fallen and *Scatophaga furcata* Say were also parasitised by *Aphaereta*.

Eucoila sp. was primarily a parasite of *Sarcophaga* spp. and occurred at a fairly uniform rate throughout the summer, the rate being about 5%. *Musca* was attacked at a rate of 1%, and *Orthellia* was not parasitised by this cynipid.

Xyalophora quinquelineata was a parasite of *Sarcophaga* spp. and attacked these flies at a rate of 7%. This cynipid wasp did not attack the *Orthellia* and only one specimen of this parasite was dissected from over 18,000 *Musca* puparia. Neither *Eucoila* nor *Xyalophora* were recovered from maggots taken during May.

Aphaereta emerged from the puparia 12-15 days after fly pupation, *Xyalophora* from 19-34 days, and *Eucoila* from 28-48 days.

The cynipids were rather specific in the species of fly attacked, both the *Eucoila* and *Xyalophora* being primarily parasites of *Sarcophaga*. Another cynipid, *Sarothrus caniculatus* Hartig, was reared only from *Paregle* puparia. *A. pallipes* was found to parasitise all species of Diptera collected. In the case of *Musca autumnalis*, parasitism amounted to as high as 100% in some collections.

DIAPAUSE AND RELATED PHENOMENA

SEVERAL TYPES OF INDUCTION AND COMPLETION OF ADULT DIAPAUSE

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In this paper the author points out, on the basis of his own investigations (on 2 species of coccinellids and 4 species of bugs) and records in the literature, the main types of induction (A) and completion (B) of the imaginal diapause in insects.

A.I. Obligatory diapause of univoltine species: even under completely favourable conditions diapause is entered by the whole population. This is comparatively rare. (*Eurygaster integriceps*—Iran, *Ceuthorrhynchus*—Netherlands.)

A.II. Facultative diapause of multivoltine species with a uniform tendency to multivoltinism in the entire population occurs more frequently. This tendency appears in the laboratory under optimum conditions. Under natural conditions potential multivoltinism

can be obscured by the dependence of the life cycle on the yearly course of environmental conditions. (*Pyrrhocoris apterus*, *Lygus rugulipennis*—Czechoslovakia.)

A.III. Perhaps most common is the intermediate type between the above two types, which occurs usually in the boundary regions between their distribution areas. The incidence of diapause under identical conditions is different in individuals of one population. In such cases a partial second generation occurs under natural conditions. Even under laboratory conditions conducive to continuous breeding, a certain percentage of adults enter diapause, often decreasing in the course of continual breeding. Presumably this is due to selection in favour of non-diapausing individuals. (*Coccinella septempunctata*—Bohemia, *Aelia acuminata*—Slovakia, *Leptinotarsa decemlineata*, *Phytodecta olivacea*—England, *Anthocoris sarothamni*—Scotland, *Anthonomus grandis*—southern U.S.A., *Hypera postica*—U.S.A., *Lixus junci*—eastern Mediterranean.)

Until recently only cases of hibernation imaginal diapause of "long-day insects", spring or early summer breeders, were known. Recently a number of cases of aestivation imaginal diapause in "short-day insects" have been recorded. (*Galeruca tanaceti*—England, *Limnophilus bipunctatus*—Czechoslovakia, *Nebria*—England, *Ceuthorrhynchus* and *Psylliodes*—Netherlands.)

B.I. Very often specific conditions, usually low positive temperature, were found to be necessary for the completion of diapause. Under natural conditions such requirements are satisfied usually before the beginning of winter, when the first phase—the phase of diapause development—comes to an end. Then development is inhibited directly by adverse environmental conditions. In the second phase it is possible to bring about normal development by transferring the insects to favourable conditions.

B.II. In another case, rarely recorded (*Pyrrhocoris apterus*—Czechoslovakia, *Lygus rugulipennis*—Germany, Czechoslovakia), reproduction can be resumed by transferring the insects to conditions suitable for normal development, i.e. in "long-day insects" by the effect of higher temperature and long photophase. There are two possible explanations: either the arrest of development remains under the control of the inducing factor, or the environmental conditions for diapause development and for the normal development are nearly identical. It is not excluded that by further investigations some cases of the imaginal diapause will be shifted from the B.I category to the B.II. Recently more evidence has appeared to indicate that the function of cold in diapause development can be replaced in "long-day insects" by long photophase.

B.III. An extreme idea of the arrest of development during diapause is a hypothesis for which Precht this year coined the term "endogenous circa-annuus rhythm", and according to which the mechanism involved should be entirely independent of environmental conditions.

Often there is misusage of the term diapause. This can be attributed often to the second phase of hibernation, when the normal development is inhibited directly by unsuitable environmental conditions, and also to diapause where the development is inhibited by a certain photoperiod. In both cases development is resumed by transferring the insect to suitable environmental conditions, which is not typical of diapause in the strict sense. Furthermore, there are numbers of arrests of gonad development which must be expected to be controlled by the same neurohumoral mechanism as in diapause development. It would be rather strange to call some of them diapause (prolonged immaturity of migrating insects, inhibition of the maturation of gonads in rabbit fleas unless they fed on pregnant females, regression of gonads in bark-beetles migrating from one tree to another). A similar mechanism occurs in starving insects or those feeding on alternative food.

The comparison of the cases of adult diapause studied supports (in accordance with the Symposium on Diapause—London 1962) the usage of the term diapause in a loose sense, for two reasons: (1) Such arrest of development as sets in obligatorily in the adult stage and synchronises the life-cycle with seasonal changes of environment by reaction to certain stimuli, which do not directly inhibit the development, cannot be called quiescence; (2) In practice, the word diapause in title will enable registration of papers. Of the papers recorded in Biological Abstracts during the last nine years more than 95% of cases of the arrest of development in insects were indicated by the term diapause, while the term dormancy is almost exclusively used for plants.

This paper is a condensed part of a review which will be published elsewhere.

FACTORS AFFECTING THE DIAPAUSE AND NUMBER OF GENERATIONS OF EUROPEAN CORN BORER (*PYRAUSTA NUBILALIS* HÜBNER)—INFLUENCE OF FOOD AND LIGHT

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P. nubilalis is a univoltine species in Yugoslavia, diapausing as a full grown larva. Only a small number of specimens which develop at the apical part of maize or in hemp have two generations. The number of generations in different regions is said to be genetically determined and this induced us to investigate the population in Yugoslavia.

1. *Number of generations depending on diet.* Using larvae from eggs of a univoltine generation, the diet was changed in one group and the illumination in a second. Leaves of *Salix* sp., *Canabis sativa*, *Zea mays*, *Tilia* sp., *Sorghum halepensis* and *Robinia pseudacacia* were used as food.

It was proved in repeated experiments that it is possible to obtain another two generations on willow leaves and hemp. On maize, lime and sorghum the caterpillars which were fully fed, died or in some cases, stopped feeding. Caterpillars given *Robinia* died without leaving any trace of damage on the leaves.

The caterpillars which were obtained on willow leaves in the third generation developed with great difficulty and perished in great numbers. These results suggest that the duration of illumination has, independently from the feeding regime, certain significance as regards the process of metamorphosis and of entering the diapause. The results also indicate that with caterpillars fed on willow fewer specimens enter diapause after the first and second generations.

Experiments on influence of duration of illumination took place with the second generation fed on willow during July. They showed that the greatest per cent of pupae was formed in experiments with permanent illumination, a smaller number in usual July daylight conditions, while the smallest number were formed under conditions in which daylight was artificially reduced to 8 hours. In the last experiment we found that migration is intensified and that larvae leave the food and die.

2. *Effect of light duration on pupa formation.* Hibernated larvae were used at different temperatures and different duration of illumination. Experiments lasted from the middle of March to the end of September, with illumination for 18 hrs. at 10°C, 15°C, 20°C, 25°C, and for 6 hrs. at 25°C. As a control pupa formation was observed in the field.

In all experiments pupae and imagines were produced. At 10°C the process of pupation lasted longest: the first were formed after 34 days and the last from the generation which survived through the winter were formed after 172 days; 29% of larvae formed pupae. At 25°C (18-hr. day) the period of pupa formation was shortest (23 days with 73% of formed pupae). At a constant temperature of 25°C with the larvae exposed to a six-hour day from April, only 1% formed pupae, while most of the larvae died.

Conclusions. Number of generations under constant conditions is dependent on food of larvae. Different feeding makes specimens from a univoltine population either univoltine, bivoltine or polyvoltine.

Illumination applied to larvae of second generation determined formation of a third generation. The greatest number of pupae was formed in experiments with permanent illumination. Light is of great importance for the interruption of diapause. Artificial prolongation of the day at even 10°C causes formation of pupae and emergence of adults: the higher the temperature, the larger the number of pupae.

IMAGINALDIAPAUSE BEI DEN IN PERIODISCHEN GEWÄSSERN LEBENDEN TRICHOPTEREN

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Beim Studium der Entwicklungszyklen von Trichopterenarten *Limnephilus rhombicus* L. und *L. stigma* Curt. haben wir festgestellt (Novák und Sehnal 1963), dass beide Arten in der Tschechoslowakei nur eine Generation haben. Die Imagines haben eine ziemlich lange Lebenszeit und fliegen in der Natur vom Mai bis Oktober. Die Weibchen überleben die Sommerperiode mit unreifen Gonaden und legen ihre Eier erst Ende August bis Oktober ab.

Bei weiterem Studium haben wir ermittelt, dass solcher Entwicklungzyklus besonders für diejenigen Trichopterenarten charakteristisch ist, welche als Larven in periodischen Gewässern ihre Metamorphose durchmachen. In den Naturbedingungen der Tschechoslowakei leben in den periodischen Gewässern besonders folgende Arten: *Limnephilus griseus* L., *L. auricula* Curt., *L. sparsus* Curt., *L. stigma* Curt., *L. vittatus* Fabr., *L. bipunctatus* Curt., *L. flavicornis* Fabr., *Grammotaulius atomarius* Fabr., *Glyphotaelius pellucidus* Retz. und *Nannophryganea minor* Curt. Alle diese Arten schlüpfen in den Niederungen im Mai. Die Weibchen aller dieser Arten haben nach dem Schlüpfen ganz unreife Gonaden. Bei der Züchtung der Imagines im Laboratorium zeigten alle diese Arten eine ziemlich lange Lebensdauer von 100 bis 180 Tagen. Auch in der Natur können die Imagines dieser Arten vom Mai bis September oder Oktober gesammelt werden. Um die Reifung der weiblichen Gonaden kennenzulernen, wurden die Weibchen, welche in der Natur in regelmässigen monatlichen Zeitpausen gesammelt wurden, seziert und der Reifezustand der Ovarien verfolgt. Es wurde festgestellt, dass die Reifung der Gonaden in den Frühlingsmonaten bei allen Weibchen, deren Larven sich in periodischen Gewässern entwickeln, gehemmt wird und dass die Weibchen erst im August bis Oktober ihre Eier ablegen. Eine Ausnahme bildet nui die Entwicklung der Gonaden von Weibchen derselben Arten in den Hochgebirgen. Hier reifen die Gonaden der Weibchen oft schon am Anfang Sommer, bald nach dem Schlüpfen der Imagines, welche hier Ende Juni stattfindet. So in den Höhen von 1350 m fanden wir die Weibchen von *L. rhombicus* mit reifen Gonaden schon Ende Juli und die Weibchen von *L. centralis* schon Ende Juni.

In Versuchszuchten wurde auch der Einfluss von Verkürzung der Tageslänge auf die Reifung der weiblichen Gonaden erforscht. In Thermostaten bei der Temperatur von 18 bis 21°C wurden in zwei Serien folgende Arten gezüchtet: *L. rhombicus*, *L. griseus*, *L. bipunctatus*. *Grammotaulius atomarius* und *Nannophryganea minor*. Eine Serie hatte die Tageslänge von 16, die zweite von 12 Stunden. Bei der Kurztagphotoperiode hat sich die Reifung der Gonaden aller Arten beschleunigt und im Vergleich mit den Naturbedingungen fand sie um ein bis zwei Monate früher statt. Bei einer Langtagphotoperiode kam es gar nicht zur Reifung der Gonaden. Die Weibchen lebten bis 276 Tage ohne Eier abzulegen.

Aus unserem Studium geht hervor, dass die Arten, deren Larven sich in periodischen Gewässern entwickeln, die Sommerperiode als sexualinaktive Imagines überleben. Die Gonaden der Weibchen reifen erst Ende Sommer und die Eier können erst im August bis Oktober abgelegt werden. Während der Sommerperiode leben die Imagines meistens versteckt an den Waldrändern. Nur im Frühling beim Schlüpfen und im Herbst bei der Eiablage fliegen die Imagines häufig in der Umgebung der Gewässer und können hier leicht gesammelt werden. Deshalb meinte man früher (Ulmer 1925, Winkler 1961), dass alle diese Arten 2 Generationen im Jahr besitzen.

Wir sind der Meinung, dass die Entwicklung mit der Diapause in der Sommerperiode für alle Trichopteren, deren Larven in periodischen Gewässern leben, charakteristisch ist. Die Diapause ermöglicht diesen Arten die Dürrenpeiiode in den Sommermonaten, bei welchen fast alle periodischen Wasserresorvoiren austrocknen, zu überleben.

Auf die Termination der Diapause hat den grössten Einfluss die Verkürzung des Tages im Spätsommer. Ausserdem spielt auch die Temperatur, wie es bei den Diapauseerscheinungen normalerweise ist, eine bedeutende Rolle.

UNUSUAL DIAPAUSE IN THE GENUS *TROGODERMA*

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Trogoderma parabile Beal is a minor pest of stored cereals and seeds. When larvae are kept after hatching in a small, but nutritionally sufficient, volume of food (0·7 cc. of wheatfeed in darkness) the development of most of them is arrested at maturity (1).

Several facts indicate that the conditions in which this arrest takes place are favourable for larval development. All larvae reached mature size in about the same time (4-6 weeks). They ate only about 9 per cent. (by weight) of the food, which was not unduly polluted with faecal pellets. Weekly renewal of the food during development did not prevent the arrest, but arrest was rare in groups of 100 larvae on 70 cc. of food, *i.e.*, with the same amount of food per larva, but a greater total volume of food. In quantities of food above about 1 cc., progressively fewer larvae entered diapause (fig. 1). Thus the arrest can be termed a facultative diapause in response to restricted space.

Diapause was induced at all temperatures that allowed development. Diapause larvae seldom hid in crevices between pieces of card on top of the food as they do in *T. granarium* Everts. Although they fed and moulted occasionally over a period of 2 years, they progressively lost weight. Spasmodically, a few pupated and some died. Early in diapause, the provision of a large amount of food terminated the diapause, but this became gradually less effective, and completely ineffective after 1 year (fig. 2).

Although no observations have been made in warehouses, or in natural habitats such as bees' nests, it seems possible that the diapause delays pupation in such places where the food supply is limited. There is much to learn about this diapause: the effects of features such as daylength are being investigated.

The diapause of *T. parabile* differs in many ways from that of the only major pest in the genus, *T. granarium* (2). In *T. granarium*, which can complete its development at temperatures between 20 and 41°C, diapause occurs at 30°C and below, being most frequent towards the low end of the scale. It is also induced by the accumulation of faecal pellets in the food—a symptom of the deterioration of the food. Diapause larvae cluster in crevices. The diapause is terminated by a substantial increase in temperature, with or without exposure to cold, but the provision of fresh food is less effective. Since in other respects the biology and rate of increase of the two species are very similar, it seems likely that the type of diapause may play a prominent role in determining the difference in pest status of the two species.

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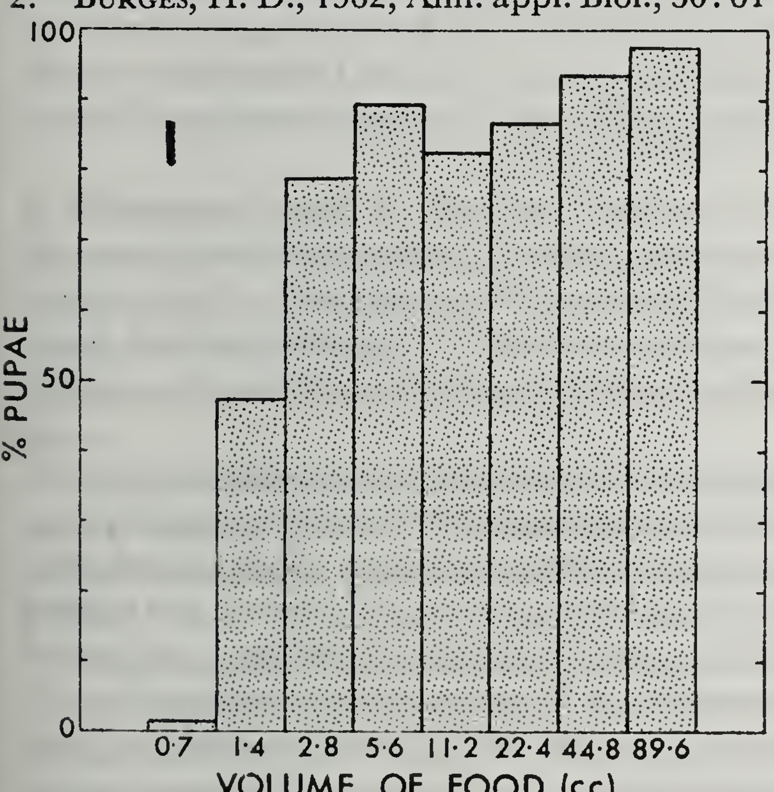

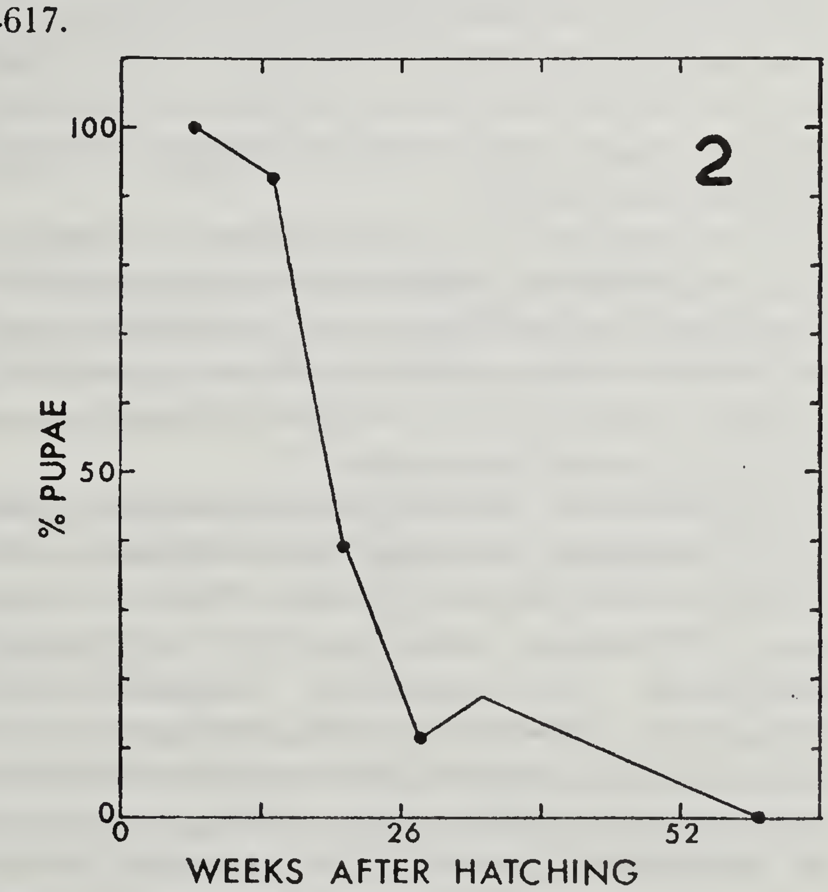

Figs. 1 and 2. Diapause in *Trogoderma*.

COMPARATIVE STUDIES ON THE INFLUENCE OF ENVIRONMENTAL FACTORS UPON DEVELOPMENT AND OVERWINTERING OF CERTAIN COLEOPTERA AND HETEROPTERA

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Autecological studies were made of insects on agricultural land, to get a better understanding for synecological correlations. Some aspects of more general interest emerged.

Influence of food upon development. *Lygus* bugs are usually placed among phytophagous insects. If water was supplied these bugs could be reared from larva I to imago by feeding them only with aphids and chopped mealworms. With animal food they developed just as well and quickly as with plant juices (1). The reverse phenomenon, i.e. development of zoophagous insects on plant material was achieved in cantharids, though to a lesser degree. The rearing of *Cantharis* species succeeded to larva IV or V on a diet of soaked grains of wheat. A few individuals reached the last instar, but died before pupating. Some larvae of *Rhagonycha fulva* could be reared to pupa or even imago on wheat grains (3).

The chrysomelid *Gastroidea polygoni* indicated differences in the food value of Polygonaceae:

Polygonum aviculare	→ development to maturity; maximal egg number
P. convolvulus, *Rumex crispus*, *R. acetosa*	→ to maturity, but reduced egg number (average)
P. persicaria, *R. obtusifolia*	→ development to imago without maturing gonads
P. sachalinense	→ larva I dies, development from larva II to imago possible
Rheum sp.	→ no larval development, adults hardly feed in absence of other food
Fagopyrum esculentum	→ not eaten by larvae or adults. Leaves dipped into juice of *P. aviculare* were eaten, but later the beetles died (2).

Among staphylinids *Tachinus* and *Tachyporus* are considered to be saprophagous. Rearing of the larvae, however, was not possible if only fed with decaying plant material and yeast. They develop to adults with animal food (aphids or Collembola) plus plant tissue (petals of Compositae) as supplementary nutriment. The adults also feed on yeast and insect eggs. The preference of eggs for food may be correlated with the behaviour of females, in moving deposited eggs on the substratum so that soil particles can stick to the glutinous shell. Eggs cleaned of earth are eaten by individuals of the same species (4).

Influence of temperature upon development. Rearing of cantharids formerly caused difficulties. Account was not taken of the fact that the succeeding larval stages change in their preferred temperature as the season progresses. The upper temperature limit of development decreases from about 30°C for larva I to about 20° for the last larval stage. Room temperature is very near the upper critical zone for complete development, while cooler temperatures considerably facilitate rearing (3).

In years with normal weather the bug *Lygus pratensis* has only a single generation in Schleswig-Holstein, while *rugulipennis* and *maritimus* have two. This is astonishing since the dependence of development on temperature hardly differs in all three species. The temperature however has a different influence upon the premature adults. In spring *pratensis* leaves its winter quarters 3–4 weeks later than the two other species, moreover it demands a longer period of ovarial maturation (1).

Hibernation. Certain processes of basic metabolism or cold hardiness during winter have been considered as adaptations of diapause. But these phenomena are not necessarily connected with each other (Precht, 1964b). Considering growth metabolism, basic metabolism and cold resistance always one type with existing adaptation can be contrasted to one lacking adaptation. The conceptions "diapause" and "quiescence" should be limited to growth metabolism. We established *Lygus* bugs and chrysomelids of the genus *Gastroidea* as species with facultative diapause; of these one generation after another can be reared, when warmth and long day are given. Chrysomelids of the genus *Lema*, staphylinids of *Tachinus* and *Tachyporus* as well as the bug *Ischnodemus sabuleti* are insects with obligatory diapause. Whereas diapause can usually be stopped by low temperature stimulus or other external factors at any time, this was

impossible for *Ischnodemus* during October and November. Up to December a seasonal arresting mechanism must be effective, which does not allow stopping of diapause. This is valid for the larval stages hibernating in the first winter of their two years' life cycle as well as for adults hibernating during the second winter (Precht, 1964a and 6).

While during the winter period, diapause proves to be a special adaptation of growth metabolism, the capacity adaptation in normal, not extremely cold temperatures refers to basic metabolism (Precht, 1960). Sudden changes of temperature after a certain time of a few days at most, cause insects with ability for a capacity adaptation to adapt to a new outer temperature, in such a way that their capacity metabolism (measured by the oxygen consumption) gets more or less independent of the change of temperature by balancing nearly to its former level. This is particularly important for insects which have to manage with their reserve material during the winter rest period. So for example a longer warm period during the winter does not cause an equally lasting higher metabolism. Some species of chrysomelids showed a capacity adaptation of metabolism during their rest period, although not during feeding time (Lühmann and Drees 1952). In *Ischnodemus* no capacity adaptation during winter can be measured (Precht 1963).

Cold resistance is a third physiological phenomenon during hibernation, which need neither be connected with growth metabolism nor with basal metabolism. In species with an adaptation to cold resistance the lower lethal temperature is shifted downwards. We proved this for larvae of Cantharidae (3), adults of *Ischnodemus* (Piecht 1963) and Staphylinidae of *Tachinus* and *Tachyporus* (4). Insects lacking resistance adaptation are forced to avoid the cold earlier or they will die, as happens to larva V of *Lygus*.

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THE EFFECT OF LENGTH OF DIAPAUSE ON THE EFFECTIVE TEMPERATURE SUMS NEEDED FOR COMPLETION OF POST-DIAPAUSE DEVELOPMENT IN *RHAGOLETIS CERASI* PUPAE (DIPTERA)

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Research work on diapause and sums of effective temperatures needed for emergence of cherry fruit fly (*Rhagoletis cerasi* L.) was a part of the study of its biology and ecology. One of the purposes of the study was to work out methods of the exact estimation of the time of emergence for timing the necessary sprays. Summing the effective temperatures seemed to be a good solution as it allowed one not only to estimate but also to predict the time of emergence.

In the literature, different statements were found concerning cherry fruit fly developmental requirements. The developmental zero was taken by different authors as 0°C, 7°C and 10°C and the sums of effective temperatures needed for emergence varied from 190° to 700°C.

The results of the work may be summarized as follows:

No flies, or only very few, emerged from pupae kept, when in diapause, at −10°C, −5°C, +10°C and +15°C. Temperatures of 0° to 5°C were most favourable for pupae to complete their diapause. Two and half months was the shortest period of diapause required to get any emergence and four months appeared to be optimal. Diapause could even be completed at higher temperatures when the pupae had been exposed for some time at the

beginning of diapause to 0°C to 5°C. This proved that low temperatures are needed only in the early phase of diapause. About 10% of pupae completed their development after a two year diapause and it is possible that some may stay in diapause for three years or more.

The developmental zero for post-diapause development of pupae was found to be 7°C. The post-diapause development was quicker at higher temperatures and the sum of effective temperatures was constant when development was at 12°C or more. At a temperature of 9°C the rule of constant total effective temperature held only for the early stage of post-diapause development i.e. until pigmentation of eyes. However completion of post-diapause development could not be slowed down at 9°C as much as would be expected and the pupae required at this temperature much smaller sums.

The sums of effective temperatures needed for emergence were constant when the pupae had remained at the temperatures favourable for diapause for a period of 4 months. The shorter the period of diapause the longer was the post-diapause development and the higher the sum of effective temperatures. It should be emphasized that the sums of days of diapause and post-diapause development were constant at a given temperature. It showed that one cannot estimate the sums of effective temperatures for post-diapause development without taking into consideration the conditions and duration of actual diapause. Those two phases of development appeared to be closely linked to each other: some failure in the estimation of constant temperature sum in different climates could be caused by lack of recognition of this.

As a consequence the existing equation for the sum of effective temperatures: $K = y(x - a)$, should be changed into: $K = (y - z)\ (x - a)$, where K = sum of effective temperatures, y = number of days with temperatures above the developmental zero, z = number of days still needed for completing the diapause at the moment when temperatures increase above the developmental zero, x = actual average temperature, a = the developmental zero and hence $x - a$ = the effective temperature.

Table 1

The sums of effective temperatures (above 7°C) needed for completion of post-diapause development in *Rhagoletis cerasi* pupae

Combinations		*the sums of effective temperatures in degrees C.*		
		until eyes pigmented	*until hairs pigmented*	*until emergence*
In constant temp. room at:	9°C	172·7	203·2	224·4
	12°C	178·2	287·4	316·3
	15°C	171·4	275·8	315·9
In orchard:	Cage 1	179·7	272·6	312·1
	Cage 2	190·3	263·6	316·4
	Cage 3	186·6	not observed	313·2

WINTER SURVIVAL OF *HELIOTHIS ZEA* (BODDIE) AT 43°30′ NORTH LATITUDE IN NORTH AMERICA

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The use of a blacklight (3600 Å) insect trap for eight years has shown *Heliothis zea* moths to appear in late summer at Arlington, Wisconsin (43°30′ N. latitude) in a pattern typical of a local, nonmigrating insect. While early season flights are poorly defined with low moth numbers, the late summer flights in August and September have produced nightly catches as high as 296 individuals. This flight begins ten days to two weeks after that of *Ostrinia nubilalis* (Hübn.), a species long known to over-winter successfully in Wisconsin.

Larval attack from the first generation of *H. zea* is evident each year in early planted sweet corn but it is the second generation of larvae which comprises the major problem on sweet corn and necessitates insecticidal control. General opinion has been that this second generation arises from moths migrating from the south and are not necessarily from a small first generation derived from overwintering individuals. The suspicion that this species might overwinter in Wisconsin prompted hibernation studies which have been conducted for three years.

During three years (1962-63-64), 43% (17 of 39) to 63% (46 of 73) of test pupae were found to be alive the following spring when placed in the stanchion area of a dairy barn. This past winter, 35·0% (7 of 20) of pupae survived the winter in glass cells attached to the walls of a silage chamber in a dairy barn and 20·8% (5 of 24) survived in a pile of corn silage within this small room between the barn and silo. During all three winters, the air temperature within the test barn remained above 0°C.

Viable pupae found each spring in the test barn were held in position for subsequent development and moth emergence. In 1962, only one moth emerged on June 20 while in 1963 emergence was noted in 23 instances and occurred from June 27 to July 29. This season (1964), 13 moths emerged between June 19 and July 17 from immature stages which had overwintered in the barn and silage chamber.

Pupae buried six inches deep in the dry soil of a tobacco shed survived at the rate of 66·7% (10 of 15) during the winter of 1962-63 and at 40% (8 of 20) during the past winter. One moth emerged (7/29) in 1963 and two appeared (7/10) in 1964. Air temperatures outside the unheated and unused tobacco shed reached a minimum of −34·4° C. in the winter of 1962-63 and a minimum of −27·2° C. in 1963-64. Pupae in glass cells affixed to the inside wall of this shed survived the winter of 1963-64 at the rate of 12·5% (1 of 8) and at the rate of 30·0% (6 of 20) in a cage holding 3/4 cubic foot of soil located on the dirt floor of the tobacco shed. No moths emerged from these pupae.

Pupae buried in sand and soil in an open field showed some survival by early spring during each of two years but no moths successfully emerged therefrom. During the very cold winter of 1962-63, 84% out of 25 pupae survived when buried six inches in outdoor soil under twelve inches of hay. However, it was not possible to secure adults from such pupae.

SECTION 7.—GEOGRAPHICAL DISTRIBUTION

The following papers were read but their authors did not wish them to be published here:

Lindroth, C. (Sweden). Skaftafell, Iceland, a living glacial refugium.

Ross, H. H. (U.S.A.). Effects of Pleistocene glaciation on North American insects.

PACIFIC ISLAND AND TROPICAL THEMES

THE GEOGRAPHICAL DISTRIBUTION OF THE SOCIAL WASPS (HYMENOPTERA, VESPIDAE)

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Darlington (1) came to the conclusion that the main pattern of the dispersal of Vertebrates shows evolution of successive dominant groups in the great favourable area of the main part of the Old World tropics and spread into smaller and/or less favourable areas. Spreading can occur along three principal routes, (*a*) into temperate South Africa, (*b*) to Australia and New Zealand, and (*c*) through temperate Eurasia and North America to tropical Central and South America.

An attempt is now being made to compare this with the distribution of the social wasps (Vespidae). The Vespidae comprises three subfamilies, the Stenogastrinae, the Polistinae and the Vespinae (2).

The Stenogastrinae occur exclusively in the Oriental and Papuan areas; they form a homogeneous group which differs from the two others in a number of striking characters (2). The Polistinae are much more heterogeneous; there is a small number of Old World genera, a larger group of New World genera, and one almost cosmopolitan group, *Polistes*. The Vespinae comprises three genera: the nocturnal *Provespa* (S.E. Asia), *Vespa* (Palaearctic Oriental and New Guinea, especially in S.E. Asia and Sumatra), and the holarctic *Vespula* s.l.

Judging from their present distribution we may conclude with reasonable certainty that

both the Stenogastrinae and the Vespinae have evolved in South eastern Asia. The first group remained restricted to this part of the world, probably on account of its specialised adaptations to the tropical rain forest; the Vespinae radiated from here, but remarkably enough they did not penetrate into Australia or the tropics of Africa and America.

The Polistinae are considerably more difficult and a key question appears to be the degree of relationship of the genera of the Old and New World tropics. In many social wasps there is a more or less distinctly delimited nonsclerotized area at the anterior margin of the sixth gastral sternite which may be a scent producing organ of importance to social life.

With respect to this organ we may distinguish:

Group 1. Area absent or only faintly indicated;

Group 2. Area distinct, bare or with pubescence forming part of the pubescence of the disc of the sternite;

Group 3. Area well delimited with characteristic pubescence (differing from that on the remainder of the sternite).

It has proved of interest to examine the relations between the condition of this character and the nest structure and distribution. If we accept that the Polistinae also originated in the Old World tropics, it would follow that the ancestors of the *Polybia-Stelopolybia* complex must have spread into the New World at an early stage, for they have radiated there into a number of different genera. All these wasps build covered nests of a structural type not found in the Old World, except certain *Stelopolybia* selecting natural cavities as nesting sites. The Old World species of group 2 also build covered nests, but the general structure shows much variation and is fundamentally different from that of the New World genera discussed above.

The Polistinae of group 3 all build nests which consist of a single comb without envelope; they are the ecologically dominant social wasps of the Old World tropics, and their numbers and distribution suggest that they have replaced here the earlier forms of group 1 and most of those of group 2. The more complex condition of the pubescent area of the sixth gastral sternite suggests that they have reached the New World at a later date than those of groups 1 and 2; the fact that there was no radiation into distinct genera in this area points in the same direction. Since these presumably later immigrants into the tropics of the New World must have had to compete with the well established and diversified members of groups 1 and 2, it appears of particular importance that their invasion of the Old World tropics has been associated with the following phenomena:

(1) the genus *Apoica* has developed nocturnal habits;

(2) many *Polistes* and nearly all *Mischocyttarus* of the neotropical rain forest mimic to a most remarkable degree certain common species of the *Polybia-Stelopolybia* complex.

It may be concluded from the available data on the Vespidae that these insects fall well into line with the main pattern of dispersal outlined by Darlington for the Vertebrates.

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WORLD DISTRIBUTION OF PYRGOMORPHIDAE (ORTHOPTERA)

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The Pyrgomorphidae include 127 genera, 6 subgenera and more than 400 species. Most are tropical or subtropical, more than half the genera occurring in Africa or Madagascar. A few are incursive into more temperate latitudes (S. Europe, C. Asia, Manchuria, Japan, Cape of Good Hope, Tasmania). They are poorly represented in the New World where they do not occur north of Mexico, south of central Brazil or in the West Indies. One fossil genus is known from Europe.

Bolívar (1909, Gen. Ins. 90) recognised 14 sections in the family, but two of these have subsequently been removed from the Pyrgomorphidae. The remaining 12 are now often

regarded as tribes, the number of which has recently been increased by the transfer of genera from three other families, by the division of 3 heterogeneous tribes, and by the erection of new monogeneric tribes to accommodate certain anomalous genera. No fewer than 29 tribes are now recognized on the basis of general and phallic morphology (Kevan and Akbar, 1964, Canad. Ent. 96:1505). This large number reflects the presumed antiquity of the group which has led to much diversification—although in some features the Pyrgomorphidae are rather uniform and readily recognisable.

A very high degree of endemism amongst genera is shown by all regions except the Palaearctic (which probably obtained its Pyrgomorphidae from the south in comparatively recent times). In terms of area, the Pyrgomorphidae of Madagascar show the greatest individuality. Those of S. and C. America, Australia, and the Papuan subregion are also very characteristic, but the last occur in surrounding areas (at least one genus, clearly of Papuan affinity, is known only from the Philippines).

The Ethiopian region is by far the richest in genera (and species) and seems (with Madagascar) to be the main centre of evolution at the present time. However, southern Asiatic genera are distributed among more tribes than are the African, so that the centre of origin of the family may well have been Oriental. Rehn (1951, Ent. News, 62; 1953, Grassh. Locusts of Australia, 2) suggests that the group is basically a so-called "Gondwanaland" one. Kevan (1959, Publ. cult. Diamang, 43) also refers to their probable southern origin in Cretaceous times. It is interesting to note that the genera having what seem to be the most primitive phallic structures—separate apical parts to the aedeagal sclerites—are either from S.E. Asia (Mitricephalini, Tagastini) or from Madagascar (Pseudogeloiini). The family probably reached the Americas on two or three separate occasions and there still seems to be a link with S.E. Asia (*Yunnanites* and *Mekongiana* from S.W. China and S.E. Tibet appear to be closest to the Sphenariini).

In conclusion it may be noted that the presently accepted tribal arrangement does not differ markedly from that of Bolívar (*op. cit.*) except for the dissolution of the three tribes already mentioned. The Orthacridini are no longer found to be discontinuously distributed from Madagascar to Mexico, nor are the Poekilocerini found from Angola to Australia. Similarly the Omurini of S. America can no longer be grouped with the Old World Atractomorphini. Even the Sphenariini, which were regarded by Uvarov (1937, J. Linn. Soc. Lond. (Zool.) 40) and Rehn (1951, Ent. News, 62) as having a very disjunct distribution, are now believed to occur only in two foci (see above) for which parallels are known among other animals. The Taphronotini and Chlorizeinini, each with genera confined to Africa and southern Asia are also somewhat discontinuously distributed.

In spite of the reasonably satisfactory grouping of genera that is now possible, however, the general phylogenetic pattern of the Pyrgomorphidae is far from distinct.

DISTRIBUTION PATTERNS OF ENDEMIC PSOCIDS (PSOCOPTERA) IN THE HAWAIIAN ISLANDS

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The isolated, volcanic Hawaiian islands support about two hundred species of psocids, thirty of which are recent immigrants occurring in the lowlands and occasionally in the highlands of the six main islands. The remainder, endemic species, chiefly restricted to the highlands, usually have distributions involving only one or two islands. These are placed in two endemic genera of Elipsocidae, and the genus *Ptycta* (Psocidae) which has a related species in each of: Reunion, Seychelles, Hong Kong, Australia, and possibly Fiji.

Of the forty-seven *Ptycta* species, thirty-six (77%) are restricted to single islands; six occur on two islands (four on the closely adjacent islands Molokai and Maui); one on three islands; three on four islands and one on five islands. Kauai, the most isolated and oldest of the main islands, exhibits 100% endemicity. It would seem that for these insects, endemicity is

related to age of islands, modified by their degree of isolation, rather than to their area or elevation (2).

Ten species groups are recognisable, and using the method outlined by Throckmorton (1), a phylogeny of the genus in Hawaii can be constructed. Mosaic evolution is apparent, and it seems possible that this is due to the perpetuation of heterozygosity in rapidly evolving populations. The widespread and relatively primitive groups *oahuensis* and *apicantha* are represented on Kauai along with the divergent *kauaiensis* group. The *kauaiensis* group, as might be expected if it is an old group which evolved in isolation, shows both primitive characters and peculiar derived traits. It is suggested that the population ancestral to the *oahuensis* group also gave rise to the highly uniform *haleakaloe* group on the eastern islands, which did not reinvade Kauai. Similarly, the *apicantha* group probably arose from a population which on the eastern islands evolved into the *schisma, lanaiensis, frogneri* and *sylvestris* groups, all of which lack representatives on Kauai, and share derived characteristics lacking in extra-Hawaiian species and other Hawaiian species groups. The *frogneri* group retains traits characteristic of the *oahuensis* group, and probably diverged earlier.

The distribution patterns of the species groups over the six islands vary from the "classical" one of the *oahuensis* group with one or more representatives on each island, to the extreme case of the *kauaiensis* group, now apparently confined to Kauai. Successive colonisation and multiple invasions could explain the distribution of six of the groups, but it is suggested that the distribution of the *schisma* and *kauaiensis* groups is more readily explicable on the hypothesis that they evolved as such on Oahu and Kauai respectively. This hypothesis does not necessarily involve sympatric speciation, despite the fact that speciation on a single island is postulated. The normal cruising range of psocids is small, and topographical effects associated with vulcanism (*kipuka* formation, amphitheatre-headed valleys) and submergence (drowning of valleys) could have provided barriers resulting in the effective spatial isolation of populations on a single island.

Probably a single ancestral population reached all the islands in its early evolutionary history. Later evolution in the eastern islands resulted in the production of six lines exhibiting various degrees of diversification, none of which have reinvaded Kauai.

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THE MICROLEPIDOPTEROUS FAUNA OF THE PHILIPPINE ISLANDS

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Little is known of this fauna and the material available in museums throughout the world is limited. The present general outline is based on a preliminary survey of over 202 species of Microlepidoptera, 130 of these being endemic, 75 apodemic. Of some 133 genera only 32 are endemic and not less than 101 apodemic.

The high percentage of specific and rather low percentage of generic endemism is the most characteristic feature of the fauna; endemic species are not always strikingly divergent, as their specialisation is of a moderate extent only. There is a great number of vicarious species, differing but little from their allies from neighbouring islands. Hitherto a number of these vicariants have been confused with similar species from other faunas.

This interesting feature shows the considerable independence of the Philippine fauna. In addition it indicates that the isolation of the region must have been of sufficient duration to create numerous endemic species, but has not been long enough to cause more profound modification, nor to create many endemic genera.

The general character and relationships of the fauna are Indo-Malayan. An analysis of apodemic, heteropatric species is as follows: Of the 75 species 20 are widely distributed and therefore are not considered. Of the remaining 55 species the Philippine fauna has in common the following numbers: with India 15, Ceylon 12, Burma 2, Java 11, Sumatra 2, Borneo 8, Celebes 5, Sula Ids. 1, Malaya 1, Tonkin 3, Formosa 3, Moluccas 2, New Guinea 11,

Bismarck Ids. 3, Solomon Ids. 2, Pacific 2, Australia 3, other regions 3. These numbers, of course, allow for only an elementary idea of relationships of the faunas, the numbers greatly depending on the degree of our knowledge of respective faunas.

Surveys of the distribution of representatives of other classes and orders of the Philippine fauna agree with one another to a great extent. This agreement permitted of the subdivision of the region into biological provinces. The northern province, Luzon, must have been connected with Formosa and continental Asia in early Tertiary; animal and plant relics in the mountains bear evidence of this northern land bridge. Later connections along the eastern border of the Archipelago caused north-south directed dispersal of animals and plants. Another marked province is that of Palawan, being a continuation of North Bornean fauna. Not less than 50% of Palawan butterflies are the same as in North Borneo. This region is rather abruptly separated from Mindoro, which has a fauna of its own, with many endemisms. Of two central provinces one with Samar, Leyte and Bohol, another with Panay, Masbate, Cebu and Negros, very little material was available, except from Negros where sugar cane plantations have several introduced pests. Finally there is the province of the large island of Mindanao, with diverse topography. It is generally understood that there must have been Pliocene and Pleistocene land bridges between this, by way of Sula Ids. with Borneo, by way of Sanghi Ids. with Celebes and by way of Talaud Ids. with Moluccas and so with New Guinea.

The available material is too limited to allow of far reaching conclusions, still some representatives of all these former connections can be traced. There are species common with Formosa, others common with Borneo, e.g. the characteristic Bornean genus *Tisis* Walker (Timyridae). The Celebesian element may be represented by the numerous species of the genus *Imma* Walker (Glyphipterygidae), while of the Papuan element may be recorded the genus *Peridaedala* Meyrick (Olethreutinae) with six endemic species in the Philippines and three in New Guinea.

DISTRIBUTION OF ORDERS POLYDESMIDA AND SPIROBOLIDA IN SOME ORIENTAL ISLANDS

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The authors have examined the millipede fauna of Japan, the Riu-kiu, Taiwan (Formosa), the Philippines and Singapore Islands. The distribution of Order Polydesmida and Order Spirobolida in these islands is very interesting.

The Order Polydesmida (flat-back millipedes) contains two sub-orders, fifteen families, 425 genera and 1960 species, mainly Palaearctic but a few Indoaustralian.

113 species of Polydesmida are found in Japan, being about 61% of the total fauna of 185 millipedes. 19 species of Polydesmida are found in Riu-kiu, being 70·3% of the fauna of 26 species. 36 species are found in Taiwan, being 61·2% of 56 species. 19 species are found in the Philippines, being only 33% of the 56 species of millipedes. Only three of them are found in Singapore, two being cosmopolitan (*Orthomorpha* and *Oxidus*), and one Indoaustralian (*Platyrhacus*).

Epanerchodus is the dominant genus in Japan and may be considered a Palaearctic element. 51 species of this genus are found in Japan, 2 species in Riu-kiu and 2 species in Taiwan, but none at all in the Philippines or Singapore.

There are 12 species of genus *Rhysodesmus* found in Japan, 7 species in Riu-kiu, 6 species in Taiwan but none at all in the Philippines or Singapore. It is not as dominant as *Epanerchodus* but may be considered as the Palaearctic element.

Platyrhacus is a poorly represented genus in the Palaearctic Region, with none in Japan, nor in Riu-kiu, nor in Taiwan. Seven species (about 12% of millipedes) are found in the Philippines and three in Singapore. It may be considered as the Oriental and Indoaustralian element being dominant there.

The Order Spirobolida (snake millipedes) contain two sub-orders, five families, eighty genera and hundreds of species, mainly tropical and subtropical. None are found in Japan or Riu-kiu.

There are six species in Taiwan (12% of millipedes); *Trigoniulus* is dominant but there is one species of *Spirobolus*. 22 species (about 39%) are found in the Philippines, with none of *Spirobolus* at all. *Trigoniulus*, *Acladocricus* etc., are dominant in Oriental Region. One species of *Trigoniulus* is found in Singapore.

In conclusion, the millipede fauna of Japan and Riu-kiu is Palaearctic; that of the Philippines and Singapore Oriental, whilst the Taiwan Islands may be suggested as intermediate, connecting the Palaearctic and Oriental Regions.

MODERN FAUNISTIC INVESTIGATIONS AS THE BASIS OF ZOOGEOGRAPHIC AND EVOLUTIONARY CONCLUSIONS

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The aim of this communication is to give attention to the fact of a decrease in number of faunistic publications noted in recent decades, and to point out the great importance of faunistic research to systematics and zoogeography as well as to the study of evolution.

Faunistic research has been carried out both by professional and amateur zoologists. It is not too much to say that our faunistic knowledge, especially in west and central Europe, is due to a great number of amateurs, some of them being very good specialists. It is common knowledge that not all faunistic papers reach a high scientific standard. This circumstance as well as a rather rapid development of experimental branches of zoology, which have laid claim to be the only "scientific" research—have caused a contemptuous attitude to field investigations. Moreover, a simultaneous progress in taxonomical research, the use of more and more precise methods, have had an unfavorable effect on faunistic research carried on chiefly by amateurs. It is then, not surprising that the number of faunistic papers has been decreasing. Amateur entomologists should collaborate with entomological institutions which, in their part, should help them with their collections, libraries and instruments. A similar fall is to be observed among papers written by professional entomologists. Modern taxonomy is evidently so attractive that some authors take pride in newly erected taxa and neglect faunistic lists. Good faunistic papers are badly needed.

The application of distributional data to systematics and phylogeny is commonly accepted. Modern systematics is a synthetic discipline, based on a very wide field and immediate information plays a considerable role in it. The fauna is always changing, sometimes very quickly, according to climatic variations and changes as a result of human activity. Irreversible destructions made by man are in some countries so violent that only an immediate and rapid faunistic survey can preserve the information about the original fauna.

The factual material contained in faunistic papers can be of a considerable value for the work of other specialists. Editors should not return manuscripts giving the only reason that they comprise too much faunistic material. Such papers should serve the interests of modern systematics and zoogeography, but authors are warned against an unnecessary splitting of papers which should not be published in obscure periodicals.

EUROPE, ISRAEL AND CENTRAL ASIA

THE DISTRIBUTION OF ANTS (HYMENOPTERA) OF THE *FORMICA FUSCA* SPECIES GROUP IN EUROPE

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The *Formica fusca* group of species are predominantly shallow nested, ground foraging ants; as such their activity is more directly related to soil surface climate than that of mound building or subterranean species. The north-south displacement of overlapping species follows the same general pattern of summer climate isolines. Five species in particular with very similar habits and extensive latitudinal ranges overlap each other in sequence from north to south with fairly clearcut boundaries.

F. gagatoides Ruzs., an arctic Siberian species ranges in the west from the North Cape to the mountains of southwest Norway. *F. lemani* Bond. ranges from north-west Norway and north Finland to southeast England and south Scandinavia (also occurring in all mountain areas to the south above 250 metres). *F. fusca* L. ranges from latitude 63° in central Scandinavia to central France but also in all mountain areas of south Europe including Spain. *F. cunicularia* Latr. ranges from south Scandinavia to the north coast of Africa. *F. gagates* Latr. ranges from central France and south Germany to the Mediterranean coast.

Each pair of species taken in sequence may be found nesting side by side in certain localities. Thus *F. gagatoides* exclusive and abundant in the extreme north of Norway shares sites with *F. lemani* near the Arctic circle in Sweden and in the mountains, giving place to the latter on warmer sites but does not occur with *F. fusca*. *F. lemani* exclusive in most of Scotland gradually gives way to *F. fusca* in north and midland England where the two species may be frequently taken together but is not found in the neighbourhood of *F. cunicularia* over the main part of their respective ranges. Similarly *F. fusca* is gradually replaced by *F. cunicularia* in the south of its range or relegated to woodland shade and is seldom found at the same site as the southern *F. gagates*.

In Britain the sequence *F. lemani*, *F. lemani/F. fusca*, *F. fusca*, *F. fusca/cunicularia* has been worked out in detail and corresponds well with summer climate indices. These, calculated from meteorological data from 155 stations, are the sum of monthly mean temperatures over 49°F. multiplied by a factor for bright sunshine (2) and enable species predictions to be made for unvisited areas which have been justified by collections. The north-south species sequence is repeated altitudinally in the hill areas of southwest England and in the mountains of Europe. Indices found empirically satisfactory for oceanic Britain are less useful for alpine areas and Scandinavia where a better fit is obtained by solar radiation isopleths as calculated by Black (1). According to these south Scandinavia has much higher summer solar radiation than northwest Germany or the Netherlands. This corresponds well with actual faunal findings where for example *F. cinerea* Mayr ranges to latitude 60° in Norway, Sweden and Finland but is absent from the Netherlands, and adjacent regions only occurring from Normandy southward within the July isopleth of 425 gm/cal/sq. cm./day as in south Scandinavia.

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FLEAS AS ZOOGEOGRAPHICAL INDICATORS IN ISRAEL

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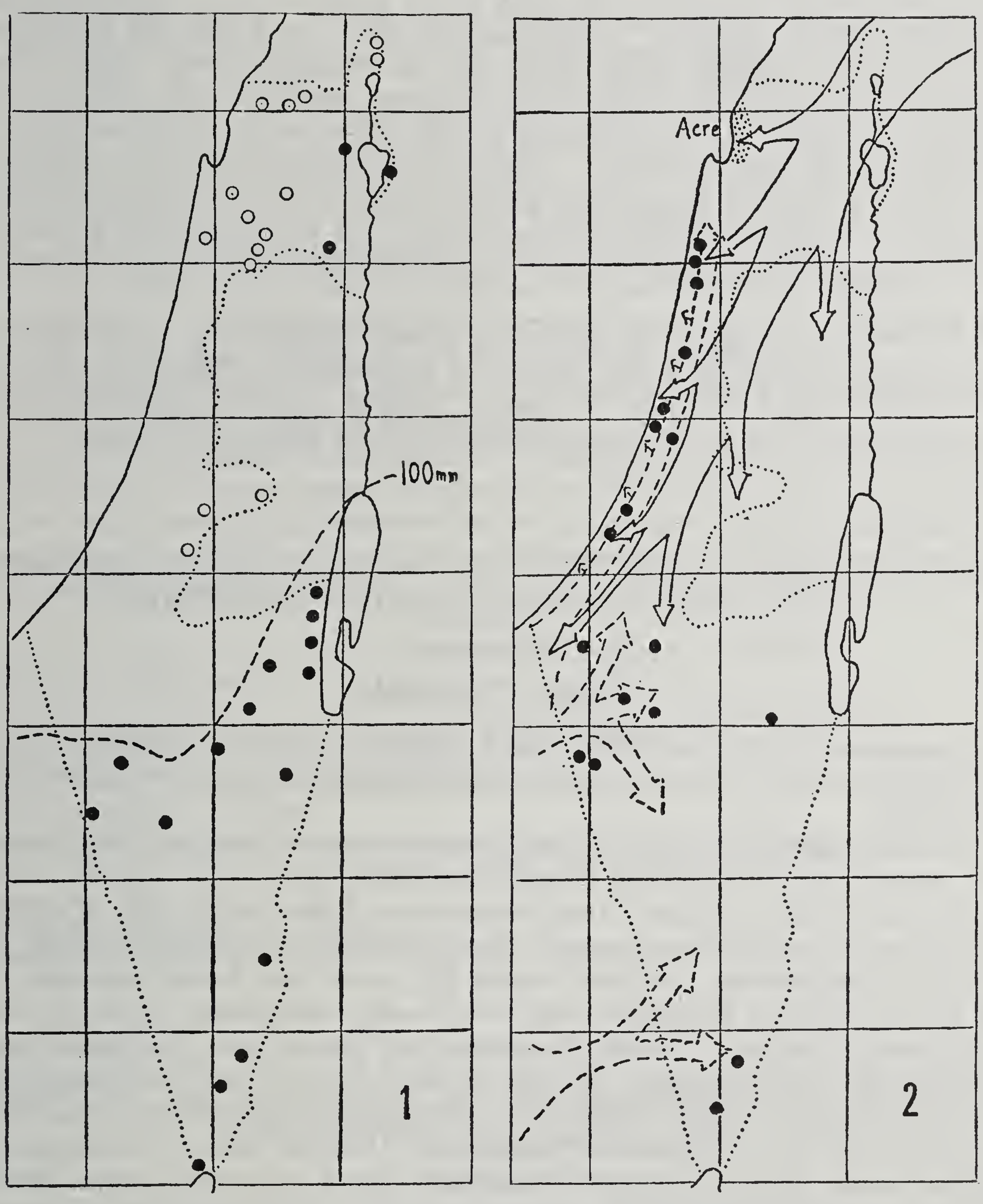
Israel

The unique geographical position of Israel on the borders of two zoogeographical Regions, namely the Palaearctic and the Ethiopian, with the influence of a third, the Oriental, causes its fauna to have an extraordinary importance for zoogeographical problems. In a relatively small area and over short distances, a great variety of climatic conditions and biotopes is encountered.

In Israel (then Palestine) Bodenheimer (1935) has applied to the fauna the phytogeographical divisions as proposed by Eig (1932). It should be emphasised that although "the zoogeographical subdivisions will be frequently based upon the botanical, they must not slavishly follow the botanical scheme and must find new principles" (Allee, W. C., and Schmidt, K. P., 1951).

Among animals ideal zoogeographical indicators should be independent of vegetational



Figs. 1-2. Recorded distributions of fleas in Israel. (1) *A. cahirinus* (circles) and *A. cahirinus* infested with *P. chefrenis* (black dots); (2) *S. cleopatrae* (black dots) and the probable ways of migration of North African gerbils (broken lines) and of *M. tristrami* (solid line). Further explanations in text.

cover, should have little power of locomotion and should show a certain degree of stenoecy. These characters are realised to a great extent in the flea *Parapulex chefrenis* (Roths.) which in Israel is a specific parasite of the two spiny mice *Acomys cahirinus* Desmarest and *A. russatus* Wagner. *A. cahirinus* is present in practically the whole country whereas *A. russatus* is restricted to the Dead Sea basin and the southern parts of the country. The distribution of *A. cahirinus* and *P. chefrenis* are shown in map 1. The restricted distribution of the flea can be explained only by the dependence of its free-living larval stages on certain bioclimatic conditions. The distribution of *P. chefrenis* divides the country clearly into two parts, the dividing line following closely the isohyet of 100 mm rainfall. The fleas have invaded the northern part of the country via the Jordan Valley, a distribution which is known also for other typical southern animals, e.g. *Echis colorata* Günther, *Atractaspis engaddensis* Haas (Reptilia) and *Cercomela melanura* (Temm.) (Aves). The distribution of *P. chefrenis* is also characterised by high summer temperatures and the cumulative maxima for June-September are near 145°C.

Parallel to the Jordan Valley intrusion of tropical elements an invasion of desert elements can be observed in the shore dunes. This can be shown by the Jirds (Gerbillinae) and their flea fauna. Most of the Israeli gerbils originated in North Africa. The origin of *Meriones tristrami* Thomas was problematic. The jirds of the sandy areas are usually infested by the flea *Synosternus cleopatrae* (Roths.). *M. tristrami* from sandy areas may also be infested by this flea, in other areas it usually carries its specific flea *Nosopsyllus iranus attenuatus* Smit. An investigation of the shore dunes showed that in the dunes of Acre (North of Haifa), *M. tristrami* is the only jird present. In this population *N. iranus attenuatus* was collected and *S. cleopatrae* was conspicuous by its absence (map 2). This is a circumstantial proof for the northern origin of *M. tristrami*—only historic reasons, indicating the way of the jird's migration, are responsible for the absence of *S. cleopatrae* from the dunes of Acre. If *M. tristrami* had followed the path from Africa, there is no reason why it should not have carried with it *S. cleopatrae* to the northern dunes.

The following zoogeographical picture of Israel emerges from these observations: a northern, mainly mediterranean part into which penetrate also Palaearctic steppe elements (e.g. *M. tristrami*) and a southern arid part. Tropical elements invade the north of the country via the Jordan Valley and eremic elements via the western shore dunes.

ZUR KENNTNIS DER KOLEOPTEREN MIT BOREOALPINER VERBREITUNG IN DEN TSCHECHOSLOWAKISCHEN KARPATHEN

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Die vorliegende Mitteilung bringt einige Angaben, die für die Erkennung der boreoalpinen Koleopteren der tschechoslowakischen Karpathen aus dem oder jenem Grund von Bedeutung sind.

1. *Bembidion difficile* Motsch. Die Art lebt nicht nur in der Hohen und Niederen Tatra vor (2, 3), sondern auch im Gebirge Kleine Tatra (10).

2. *Patrobus assimilis* Chaud. Das Vorkommen dieser Art in den Karpathen wird allgemein als sehr zweifelhaft angesehen. Die Richtigkeit der einzigen Angabe, nach der diese Art bei Dobšiná-Höhle gefunden wurde (8), wurde mit Recht bezweifelt (3). Die Revision des betreffenden Exemplares hat diese Zweifel vollkommen bestätigt. Es handelt sich um *P. atrorufus* Ström. Von den Karpathen liegt jedoch noch eine andere Angabe von Kult (6) vor, der zwei Exemplare mit dem Fundort "Orava" aus der Sammlung Roubal meldet. Die Exemplare wurden seinerzeit von Roubal (8) als *P. excavatus schaubergeri* Roub. von "Orava, Suchá hora, Sphagnetum" angegeben. Ein von diesen Exemplaren /♂/ wurde revidiert und seine Zugehörigkeit zu *P. assimilis* Chaud. liegt ohne jeden Zweifel. Der Fundort ist ein hochgelegener (750m) Sphagnum-Moor. Dieser Moor ist der einzige bisher bekannte Fundort dieser Art in den Karpathen überhaupt.

3. *Olistherus substriatus* Gyll. Auf den boreoalpinen Charakter der Verbreitung dieser Art hat als erster Horion (4) aufmerksam gemacht. Von den slowakischen Karpathen sind

eigentlich nur zwei Fundorte bekannt: Niedere Tatra (8) und Naturschutzgebiet Dobroč-Urwald im Slovakischen Erzgebirge.

4. *Geodromicus longipes* Mannh. Die Art ist von der Liste der boreoalpinen Koleopteren zu streichen. Es handelt sich um einen Komplex von untereinander sehr ähnlichen Arten. Die nordeuropäischen Populationen sind von jenen der mitteleuropäischen Gebirge spezifisch verschieden. Die Form der Alpen (*G. kunzei* Heer) steht der ursprünglichen nordeuropäischen Art (*G. longipes* Mann) viel näher als die Form der westlichen Karpathen (*G. dunieli* Smet.). Die Meldungen aus den Ost-und Südkarpathen beziehen sich höchstwahrscheinlich auf *G. puncticollis* Weise. Diese Art kommt in Westkarpathen nicht vor und hat mit dem Artenkomplex von *G. longipes* Mannh. überhaupt nichts zu tun.

5. *Autalia puncticollis* Sharp. Die Art kommt in den slowakischen Karpathen nicht nur in der Niederen Tatra: Ďumbier (8), Chopok (11), sondern auch in der Hohen Tatra: Belanské Tatry vor.

6. *Oxypoda nigricornis* Motsch. Die Zugehörigkeit dieser Art zum boreoalpinen Verbreitungstypus liegt ohne jeden Zweifel (5, 12). Von den Karpathen bisher nur aus der Hohen Tatra bekannt.

7. *Silpha tyrolensis* Laich. Die Art besitzt in den Karpathen ein ganz isoliertes Vorkommen im Gebirge Kleine Fatra. Die alte Angabe von Branscik (1) vom Gipfel Malý Kriváň wurde jedoch bezweifelt (2, 3), da die Art später nie wiedergefunden wurde. Aus letzter Zeit liegen jedoch zwei weitere Meldungen aus diesem Gebirge vor, diesmal vom Gipfel Chleb (9). Die neuen Funde bestätigen überzeugend die alte Angabe von Brancsik.

8. *Corymbites rugosus* Germ. Das Vorkommen dieser Art in den Karpathen, welches nicht allgemein bekannt ist, scheint auf die Hohe Tatra beschränkt zu sein (7, 9).

Die Liste der boreoalpinen Koleopteren der Karpathen wird sicher um weitere Arten bereichert, deren Zugehörigkeit zum boreoalpinen Verbreitungstypus bisher nur vermutet wurde oder unbekannt geblieben ist. (z.B. die Staphyliniden *Eudectus giraudi* Redt., *Bryoporus rugipennis* Pand., *Atheta diversa* Sharp und *Atheta brunneipennis* Thoms.).

Der Unterschied zwischen den Alpen und den Karpathen, was die Zahl der boreoalpinen Koleopteren betrifft, bleibt weiterhin ziemlich gross.

Die Zahl der boreoalpinen Koleopteren wird allgemein im Licht der neueren Erkenntnisse deutlich höher sein, als es bisher gewöhnlich angeführt wird. Von den Staphyliniden sind z.B. als echte Boreoalpiner folgende Arten anzusehen: *Olistherus megacephalus* Zett., *Omalium strigicolle* Wank., *Bledius litoralis* Heer, *Gnypeta coerulea* Sahlb., *Atheta excelsa* Bernh. und *Oxypoda skalitzkyi* Bernh.

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THE PRINCIPAL REGULARITIES OF GEOGRAPHICAL DISTRIBUTION OF COLEOPTERA IN MIDDLE ASIA

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The author undertook the task of investigating the composition and origin of the terrestrial fauna of Middle Asia. He analysed for this purpose by a comparable method the distribution of 5 families of Coleoptera: Carabidae, Histeridae, Scarabaeidae (s.lato), Tenebrionidae and

Cerambycidae. The data on some other groups of Insects (Dermaptera, Acrididae, Scoliidae etc.) and Vertebrata (Sauria, Rodentia) were taken for comparison. All the investigated groups selected were the most thoroughly studied ones in the fauna of the U.S.S.R. More than 500 genera including more than 2500 species (among them 397 genera and over 2200 species of Coleoptera) were examined. The genus was selected as the principal taxonomic unit for analysis. This analysis shows that the distribution of the great majority of studied groups is subjected to the general rules.

The high percent of endemics not only of specific rank but also of generic, is very characteristic of the fauna of Middle Asia (85 geneia and nearly 1500 species among the studied families of Coleoptera). This proportion is still higher in several groups (Tenebrionidae, Gomphomastacinae etc.). It is important from the practical point of view, that endemics form a considerable part of the noxious fauna. There are many endemics among beneficial animals too.

It is possible to establish three principal centres of endemism and speciation viz.: Turanian (desert), Irano-Bactrian (mountain-desert) and Afghano-Turkestanian (mountainous).

The Middle-Asiatic fauna includes, besides this great endemic kernel, also numerous species and genera, widely distributed in the vast region of "Ancient Mediterranean" or in other districts of the Holarctis and sometimes in the tropical areas of Africa and Asia.

The abundance of specialised endemics of high taxonomical rank in the sandy desert and in the mountainous districts of Middle Asia is especially significant. These facts are in contradiction with the opinion often expressed about the recent geological age of these landscapes in the region studied.

Present biogeographical and palaeogeographical data show that Middle Asia is one of the most important and most ancient (at least from the Neogen) centres of autochthonous formation of the arid fauna. The faunas of other arid regions of Holarctis Central-Asiatic and North-African in particular—are younger and include numerous species and genera, migrated from the Middle-Asiatic centre.

Side by side with such endemic forms many species live in Middle Asia, having vast areas of distribution and having penetrated there during Glacial and Post-Glacial time, and in many cases in connection with the activity of man.

Although the Quaternary period was—as in the other parts of Holarctis—the time of extremely intensive processes of change of geographical environment and reorganisation of the fauna, the autochthonous kernel continued to take the principal part in its composition.

The studied material was used as the basis for the more detailed zoogeographical division of Middle Asia and of the whole Irano-Turanian area. The latter area is one of the three principal subdivisions of the extensive Saharo-Gobian desert subregion (Eremian zone) of Holarctis.

AN ECOLOGICAL AND ZOOGEOGRAPHICAL ANALYSIS OF THE ESTONIAN FAUNA OF CARABIDAE (COLEOPTERA)

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On the basis of a comparative and historical analysis of the 276 species of Estonian Carabidae two main types of ranges—*Boreal* and *Paratethical*, are distinguished, each with five subtypes. In accordance with the prevailing dynamics of the range, the cold-resisting *arctodynamic* and the *thermophilous tethodynamic* species are distinguished in each group. Among the latter we may distinguish in their turn the *boreodynamic* species.

The Transpalaearctic, European, Eurasio-W. Siberian and Euro-Siberian subtypes cover the majority of the species (65%). The Eurasio-E. Siberian, Europontic, Holarctic, Sibero-Baltic and Euro-Mediterranean subtypes account for 6-8% of the total.

69% of the species show a tendency to latitudinal (E $\rightarrow$ W), 31% to longitudinal (S $\rightarrow$ N) dynamics.

36% of the Boreal and 65% of the Paratethic type species attain limits of their range in

Estonian territory. The majority of these are tetho- and boreodynamic species, which reach their northern boundary.

34% of the species have flourishing populations. These include 45% of the arctodynamic species in the Boreal and 77% in the Paratethic type, but only 19% of the boreo- and tethodynamic species. Species of open countryside predominate with 80-90% of the total fauna. About half the species prefer the shores of the inland waters. Next in importance is the coastal area. The Euro-Siberian, Sibero-Baltic and European subtypes are rich (48-26%) in fen and bog species. The forest species are more than twice as numerous in the Boreal as in the Paratethic type.

On the whole the most successful, ecologically plastic and euryvalent element is the East-Palaearctic group, and the arcto-dynamic species in general. The West-Palaearctic element is less successful, more stenovalent and richer in tethodynamic species. Most evenly distributed over the whole area are the species of the Holarctic and Euro-Siberian subtypes. The central part of the mainland has no Europontic or Euro-Mediterranean element.

The post-glacial age of the Estonian immigration fauna ranges from 15,000 to 3,700 years according to the locality. An analysis of the fauna reveals three basic stages in its evolution.

During the first stage from the Gothiglacial to the concluding phase of the Yoldian sea it was the continental refuges of the Archipalaearctic which made the largest contribution to the formation of the fauna. This wave of immigration reached Estonia from the E and NE. The bulk of the fauna was composed of the arctodynamic species of the Holarctic, Transpalaearctic, Euro-Siberian and European subtypes. This period was characterised by the wholesale elimination of the arctic and boreoalpine species.

In the second period, the stage of the Ancylus lake and the Littorina, the western part of the mainland and the archipelago emerged from the sea. In the conditions of the Atlantic climatic optimum the area was overgrown by forest. The vast bulk of the tethodynamic species, which moved in from the SE and SW, arrived from the Mediterranean Refuge. The fauna was enriched mainly by the species from the Euro-Mediterranean, Europontic and Eurasio-E. Siberian subtypes. The variety of species now attained its maximum. Afforestation drastically curtailed the habitats of the open countryside species. The predominantly spruce forest belt of Intermediate Estonia has remained to the present day the chief obstacle to expansion, splitting the ranges of many species into two detached part-ranges.

The last period of about 3,000 years witnessed the steady reduction of the tethodynamic species and their retreat southwards. At the present time the weakly represented Euro-Mediterranean, Europontic and boreomontanic elements, also the halobionts, are declining. The halophilous species are expanding in the region of the Väinameri (Little Sound) and the NW coast. The boreodynamic species are making steady progress in the northern coastal zone.

The present composition of the fauna shows Estonia to be a transitional area between the Western and Eastern Palaearctics. Although the number of West-Palaearctic species is slightly larger (in a ratio of 54 : 46%), it is the East-Palaearctic element which both constitutes the majority of the fauna and evinces superior adaptability.

THE FAUNA AND ECOLOGICAL GROUPS OF CLICK-BEETLES (COLEOPTERA, ELATERIDAE) OF MIDDLE ASIA

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At present in Middle Asia about 160 species of click-beetles are known; further investigation will probably increase their number.

The most striking feature of this fauna is its extreme endemism: nearly 70% of species are endemics. In addition there are some species with a mainly Middle Asian distribution

and others with distribution centring in Middle Asia, but represented here by endemic subspecies.

There are endemics of higher systematic rank, namely the 4 genera: *Clon* Sem., *Denticolloides* Gurjeva, *Neocardiophorus* Gurjeva, *Nyctor* Sem. et Piat. The last one is placed in a special tribe (*Nyctorini*), endemic to Middle Asia. Only one of these 4 endemic genera lives in the mountains, the other 3 are inhabitants of desert areas.

The high endemism of the Middle-Asian fauna is proof of the great antiquity and isolation of Middle Asia as an evolutionary centre.

In Middle Asia we may distinguish two main centres of endemism: the first is a desert plain, having ancient connections with Mediterranean and African faunas, and the second is mountainous, the mesophyllic forest elements taking part in its formation.

Among click-beetles living in Middle Asia and having their areas of distribution lying outside Middle Asia, the first place in abundance belongs to the European-Siberian species (firstly the forest elements, the steppe ones in a less degree), the second—to the Mediterranean species (mainly south-west-Asian) and the third place—to Indian ones.

The European-Siberian species are represented more fully in the north mountain chains of Tien-Shan, they are not distributed in Central and West Tien-Shan, as a rule. The distribution of south-west-Asian species is usually restricted only by the Kopet-Dag mountains. There are only two species connected with the Indian fauna (these are: *Lacon turkestanicus* Schw. in Tajikistan and *Tropihypnus bimargo* Rtt. in North and West Tien-Shan).

In spite of great diversity of ecological conditions in Middle Asia we can arrange the species into a small number of groups which have similar biological peculiarities. These groups consist of species, inhabiting: (1) the sandy desert; (2) the deserts with compact soils and open spaces of lower, partly intermediate, mountain zones; (3) the mountain forests; (4) the mountain meadows and steppes; (5) subalpine and alpine meadows; (6) the wide stony river banks, so specific for Middle Asia; (7) oases.

INFLUENCE OF THE PLEISTOCENE GLACIATIONS ON INSECT DISTRIBUTION

THE GEOLOGICAL BACKGROUND TO EUROPEAN PLEISTOCENE ENTOMOLOGY

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A proper appreciation of Pleistocene geology is vital to an understanding of the great changes in insect fauna which have affected Britain, Europe and much of the world during the last million years or so.

Although the "Ice Age" is associated with the Pleistocene, it is wrong to regard the two terms as synonymous. The period of time which succeeds the Pliocene is controlled by a fluctuating climate which, in these latitudes, follows a pattern as shown in fig. 1.

The curve is a rough one of relative temperature, probably too simple but bringing out the complex alternations which affected the northern hemisphere. Whether glaciers persisted at any place during a cold period depended not only on the relative magnitude of the cold cycle but also on latitude, topography and the availability of precipitation. It is likely that there were mountain glaciers in Britain during the Eburonian and Menapian but it is not until Elsterian I that we have positive evidence of ice which lay in the North Sea and at least impinged on Norfolk. After that there was a succession of *GLACIAL PERIODS* when ice, accumulating on the highlands of Britain, spread out as slow-moving sheets into central Ireland, the Irish Sea, the Scottish lowlands, central England and East Anglia. Yet England (unlike Scotland, Wales and probably Ireland) was never wholly covered by glaciers and during

the severest of climates the counties south of the Thames and Severn Estuary would support some sort of flora and fauna.

No picture of the "Ice Age" would be complete without an assessment of the milder periods. During the *INTERSTADIALS* which are shorter-lived, not very warm interruptions of the cold cycles, the extent of ice certainly decreased but may not entirely have disappeared from Britain. There were larger ameliorations of climate which are the Cromerian, Holsteinian and Eemian *INTERGLACIALS* and in these (and, of course, the modern Post-Glacial) ice completely left Britain and in Europe shrank back to the highest mountains only. There is evidence, largely biological, that the Holsteinian at its peak differed little from modern climatic conditions but the Cromerian and Eemian were notably warmer.

It will be appreciated that in the earlier part of an interglacial, deglaciated areas available for insect colonisation would be unusual in their soil characteristics. Upland areas would be largely scraped clean of soil; lowlands would be covered with tills and outwash gravels, essentially unweathered and tending at first to give base-rich soils. These factors must have had a direct effect on some beetles (e.g. the *Carabidae*) and on many more an indirect effect because they exercised a control over the nature and density of the colonising vegetation.

In several ways the geologist can assess some of the physical characteristics of the Pleistocene without recourse to arguments based on the mode of life of organisms. The very presence of large ice sheets spreading southwards into north Russia, north Germany, Holland, England and northern U.S.A. carries with it certain clear implications about the lowering of mean annual temperature. In land beyond the limit of glaciation, the presence of disturbed deposits indicating deeply penetrative frost and often "permafrost", may necessitate depression of the mean isotherm by as much as 13°C. Physical evaluation of the interglacials is harder but where soils were developed, they can tell us something of temperature and rainfall. Work on the $^{18}O/^{16}O$ ratio of foraminifera tests in core samples from the floor of the Atlantic gives evidence of temperature fluctuations in the ocean matching the sequence of land changes but less in amount, as might be expected.

With climatic fluctuations of a size and speed seldom, if ever, paralleled in earth history, it is not surprising that the Pleistocene is characterised by spectacular changes in insect faunas. Obviously important in the explanation of these, especially for an island like Britain, is the

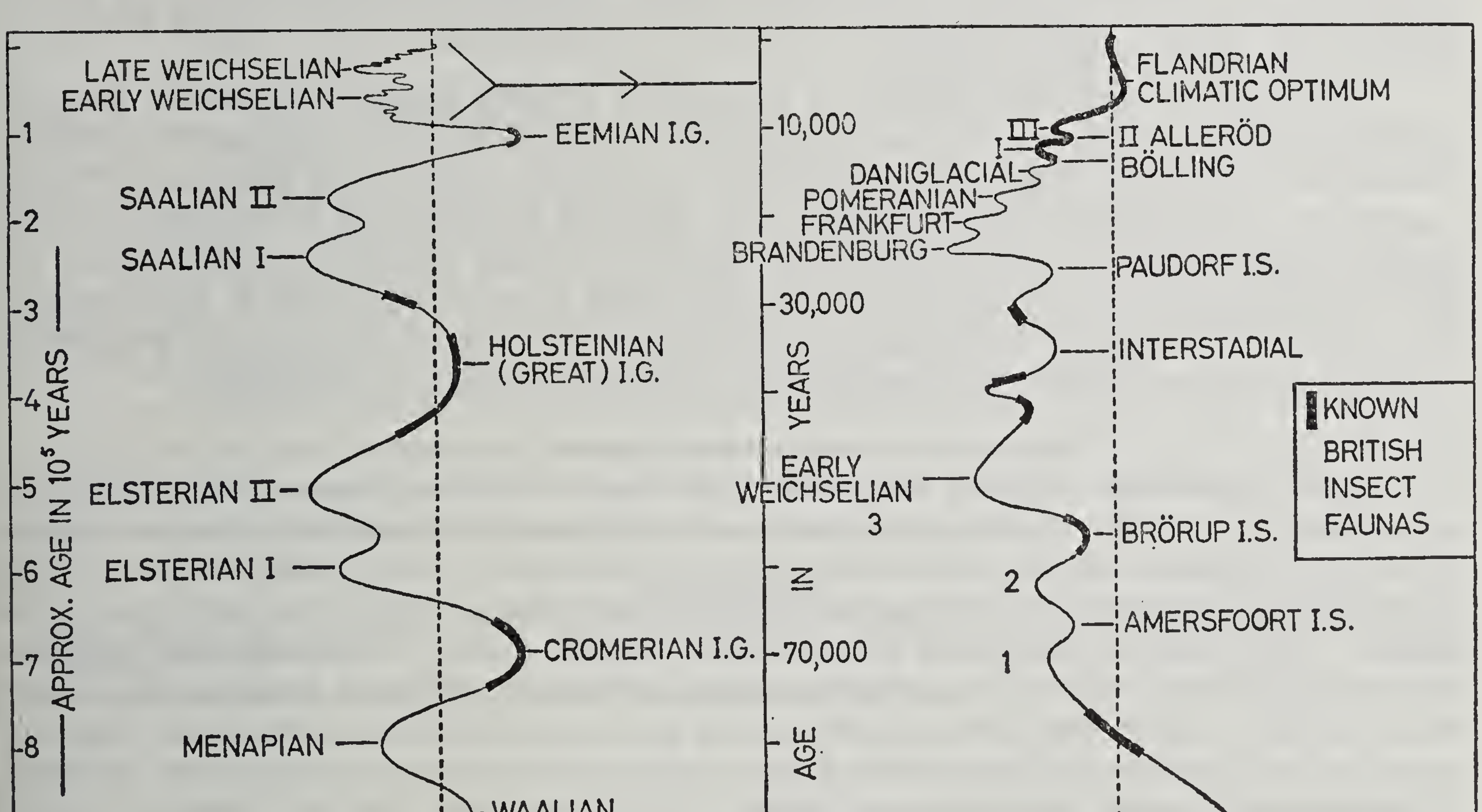

FIG. 1. Pattern of climate in period succeeding Pliocene. The nomenclature includes many synonyms, one set of stratigraphical terms only has been used.

availability of land connection with the continent. There is good evidence that the North Sea and the Channel became separated at the end of the Pliocene and thereafter I can find no evidence of the Dover Strait being re-established until the generally accepted date of 6000-5000 B.C. The land bridge probably had a minimum width of only about 20 miles in the Holsteinian and Eemian interglacials when sea-level was higher than now. During each glaciation sea level must have fallen considerably all over the world—three hundred feet is the least that can be suggested for the Weichselian—and in such circumstances the southern part of the North Sea must have been land, even if much of it was marshy. This "Doggerland" with its north shore joining Denmark to Yorkshire, is well attested for the Late-Glacial and early Post-Glacial (i.e. 12,000 to 6,000 B.C.), but I have no doubt about a similar broad land connection during all the glaciations. At times the diminished North Sea would be full of ice.

I have elsewhere questioned whether Ireland could have had connection with the rest of Britain except in the later Weichselian. If this was so, and the Elsterian and Saalian glaciations covered all Ireland, there could be some interesting problems of insect extinction and colonisation awaiting solution.

THE RESPONSE OF THE BRITISH INSECT FAUNA TO LATE QUATERNARY CLIMATIC OSCILLATIONS

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The exoskeletons of insect are very resistant to decay and are to be found abundantly in a very good state of preservation in many Quaternary deposits. They are to be found most often in peat, river silts and lake beds—in fact in any deposit where the conditions were suitable for the accumulation and preservation of plant debris. Since most of the remains were discovered incidentally by botanists studying the ancient flora, the insects were consequently neglected and apart from Henriksen's monumental thesis (2) little has been attempted by way of a systematic study of them.

I am going to restrict myself here to a summary of insect faunas from the last hundred thousand years, namely the Eemian interglacial and the succeeding Weichselian (Würm) Glaciation. This period provides evidence for an oscillation in climate from conditions so warm that the Hippopotamus could thrive as far North as the Midlands, to conditions of such extreme cold that glaciers flowing from the Scottish and Lake District mountains, filled the Irish sea and pushed southwards over the Cheshire plain to reach as far south as Wolverhampton. Minor fluctuations of temperature during this period are well known and it has been possible to relate our fossil insect assemblages to various episodes of the glaciation.

Fossil insect assemblages related to climate

Eemian (*Ipswichian or Last*) *Interglacial.* The most extensive faunas dating from this period are from two sites in the terrace gravels of the Thames, one in a foundation excavation in Tragalgar Square and the other in a sand pit at Isleworth. The Trafalgar Square fauna dates from the interglacial climatic optimum and includes a large number of relatively southern species. The fauna is dominated by scarabaeid beetles, mostly *Onthophagus* and *Caccobius* an interesting fact in view of the number of bones of large herbivorous mammals that came from the site. Some very distinctive fragments have so far defied identification; they are certainly not represented in North West Europe today and at the moment the search for them is concentrated among Mediterranean faunas. It is quite clear that the Trafalgar Square fauna indicates warmer conditions than those of the area today.

The Isleworth fauna has been more thorougly investigated but nevertheless there are fewer exotic species and the fauna looks much like that of southern England today. Two more sites of this age have been investigated, namely Bobbits Hole Nr. Ipswich, and Selsey Bill. The number of species recorded is too small for an adequate picture to be built up. But the

occurrence of the distinctly thermophilous species *Oodes gracilis* Villa at Bobbit's Hole suggests a mid-summer temperature at least 3°F above present day.

Weichselian (Würm or Last) glaciation

Brörup (Chelford) Interstadial. During an early phase of temporary amelioration of climate in this glaciation deposits of organic mud were laid down near Chelford in Cheshire. The contemporaneous insect fauna showed a very marked change from the interglacial fauna. It is characteristic of a cool temperate conifer forest with a hint of continentality. At least two species are now extinct in this country but still survive in Scandinavia. The picture of climate and ecology derived from the study of the insect assemblage is matched to a remarkable degree by botanical evidence from this site.

Full Glacial. From a river terrace on the Avon at Fladbury, Worcestershire a fauna has been found representing an extremely cold phase. Out of a total fauna of almost fifty species, fourteen are known to be extinct in these islands today. At least two appear to be entirely extinct and the rest are found in the extreme north of Europe. River terraces in the Trent drainage system at Minworth (Warwickshire) have yielded insect faunas of full glacial age that have much in common with the Fladbury fauna.

Upton Warren interstadial. Up to this phase the insects have presented a consistent picture of the climate. However, from a deposit at Upton Warren, Worcestershire, which on geological gounds and by radiocarbon dating is full glacial in age, was collected a large insect fauna which contained certain anomalies. It is clear that the general affinities of this fauna are with the Fladbury and Minworth assemblages yet it lacks some of the more arctic species and has in addition a considerable number of comparatively warmth loving species. What is more, the modern distributions of these southern species in many cases do not overlap the distributions of the northern species. No simple explanation seems possible in this case. I have suggested (1) that this mixing of species is due to a rapid amelioration of the climate—probably of relatively short duration, that permitted the incoming of the southern group without exterminating all the northern forms. The climate that best fits the requirements of the Upton Warren fauna might best be matched with that of Southern Sweden today. This conclusion contrasts strongly with the evidence from pollen counts obtained from the deposit, which showed an almost total absence of trees suggestive of tundra conditions. However the absence of trees at Upton Warren need not necessarily be due to climate. From the abundant remains of large herbivorous mammals in the deposit it is clear that the area was heavily grazed and this may well have prevented the colonization of the district by trees. In our interpretation of the conditions at Upton Warren it was the insects that forced a reappraisal of the evidence which otherwise might well have led to very different conclusions.

Late Glacial. With the final retreat of the ice into the Scottish mountains many northern insect species were widespread over the country. As recently as 10,000 years ago there were species present here which have since disappeared from Britain and are now confined to northern Scandinavia and the high mountainous districts of central Europe.

These northern species were found in association with several other species whose distribution today is in Eastern and Central Europe. Such a species is *Chlaenius costulatus* Motsch, whose most westerly population today is near Stettin in Northern Germany. This species occurs in two widely separated sites in the Late Glacial of Scotland.

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INSECTS AND POST-GLACIAL VEGETATION

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A greater understanding of the present distribution of phytophagous insects might be obtained from the information now available concerning the history of the post-glacial flora, particularly from pollen studies. In Western Europe the general picture of the spread, displacement, change and decay of the forest cover shown by this work is especially vivid In this country we are fortunate in having a general work on the "History of the British Flora" by Professor H. Godwin, which gives a striking and well-documented account of these changes. In general, speculations concerning insect distribution can lead only to plausible conjecture and evidence from fossil records is essential; but a detailed knowledge of plant history can have a sobering effect on such speculations.

Perhaps in areas where this type of information is available, certain problems concerning subspecies may prove to be more worth while investigating at the present time. For example, in the butterflies of Ireland the few endemic subspecies or forms that are recognised feed on ruderals or weeds, species of the type of plant community recorded from the late glacial period. One would expect, therefore, that insects of other groups in the Irish fauna with the same general type of ecological requirements might well repay further study concerning subspeciation. Such species of open country became of course very localised in times of forest maxima.

It would appear that all deciduous forest insects must have arrived in the British Isles only in post-glacial times. However there are a number of species associated with the deciduous forest belt which occur in Britain in a distinct form. It would seem therefore probable that these insects may well be the remains of earlier Western European forms which have been segregated in the British Isles, and eliminated in the rest of Europe. If such were the case, it would be feasible that occasional examples of the British forms might be taken as "aberrations" in Western Europe. *Cratichneumon fabricator* (F.) (Hym., Ichneumonidae) may be an example of this.

It is unlikely that adequate fossil records of many groups of insects will be obtained, but to the taxonomist speculation concerning distribution does form an ever-present background. With phytophagous insects, a knowledge of the history of the flora which is now so fully documented, is a source of information of prime importance.

THE EFFECT OF FOREST CLEARANCE ON THE DISTRIBUTION OF THE BRITISH INSECT FAUNA

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During the Quaternary one of the main factors governing insect distributions in this country was, directly or indirectly, the wide fluctuation in climate. However, since Neolithic time man's interference with the environment, particularly the destruction of the climax forest in the interest of agriculture has had a profound effect on these distributions. Evidence of this has been provided from five Post-Glacial deposits:

1. *Shustoke A* (Warwickshire). An organic gravel from the alluvium of a small stream. Dated by ^{14}C at 4,880 years B.P.
2. *Alcester* (Warwickshire). A bed of peat representing a Carex marsh, also beside a stream. Placed in pollen zone VII.
3. *Church Stretton* (Shropshire). A bog peat following lake deposits. Pollen analysis indicates zone VII.
4. *Wilsford* (Wiltshire). Material from the bottom of a deep shaft in the chalk near Stonehenge. Archaeological evidence indicates a date of c.3250 years B.P.
5. *Shustoke B* (Warwickshire). A bed of what appears to be flood refuse in the alluvium of the same stream as Shustoke A. ^{14}C dated at c.400 years B.P.

Shustoke A, Alcester and Church Stretton were deposited before the Neolithic forest clearance got under way and if aquatic species and those dependent on marsh or waterside vegetation are excluded each fauna consists almost entirely of woodland insects. Most interesting amongst these are *Rhysodes sulcatus* from Shustoke A and *Ernopocerus caucasicus* from both Shustoke A and Alcester. Both of these inhabit woodland. The host plant of *E. caucasicus* is Lime, a tree which was common at both sites but which has since declined, and *Rhysodes* lives in rotten wood, probably as a predator. Neither of these beetles is on the modern British list and their absence may well be accounted for by the destruction of a large part of their habitat, although a deterioration in climate since the post glacial climatic optimum may also have been partly responsible. Another species, *Dryophthorus corticalis,* appears then to have been widespread, for it occurs in both Shustoke A and Alcester but it has had its range so curtailed that it has only been recorded living in Berkshire.

The more recent deposits, Wilsford and Shustoke B, both contain many species indicative of open ground. The fauna of the Bronze Age site at Wilsford is one of grassland with many grazing animals. Both in numbers of species and individuals the list is heavily dominated by dung beetles, particularly of the genera *Geotrupes, Onthophagus* and *Aphodius.* Species which feed on grass roots, such as *Brachylacon murinus, Agriotes sputator* and *Phyllopertha horticola* were also present in some numbers.

In the last 400 years, since the deposition of Shustoke B, the beetles of Warwickshire appear to have undergone little change. This site contains a wealth of species which live on cultivated plants or on plants associated with agriculture as weeds. This element is quite absent from the earlier sites investigated. Grassland species and those which live in dung are well represented and, unlike Wilsford, a small number which feed on trees are also present.

Thus it will be seen that a major change has taken place in the distribution of our beetle fauna since the advent of sophisticated agricultural methods some 5,000 years ago. The once dominant forest element has become much restricted in range, although apparently not much depleted in numbers of species, whilst those beetles which were formerly confined to places where, for various reasons, trees were unable to grow, have become widespread throughout lowland Britain.

THE MAIN CHARACTERISTICS OF THE DIPTERA FAUNA OF NORTH-WESTERN EUROPE

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Diptera collected during the last decades in eastern Baltic, mainly in the Leningrad region and in Estonia, and literary data dealing with the Diptera fauna in the countries of North-Western Europe (mainly in Finland and Sweden) serve as a basis for my report.

The fauna of Diptera of these regions is rather rich, thus for Finland there are recorded as many as 4,400 species (Héllen, 1961), for the Leningrad region—not less than 3,500 species. Thus the Diptera fauna of North-Western Europe is very rich and at the same time very young. One should not forget that a considerable number of Diptera species of the present North-Western Europe fauna is connected with forests and consequently they arrived here when the said regions had become free of ice. However, this consideration does not mean that the whole pre-Glacial Diptera fauna of North-Western Europe was annihilated.

The formation of the Diptera fauna in North-Western Europe was a complex process carried out step by step, from different centres, and in different periods of the post-Glacial History. Those groups which can be regarded as relict are of special interest. Due to their ecological specificity these species of southern origin form two distinct groups connected with intrazonal landscape elements.

1. *Species connected with open territories with sandy soil.* The majority of xerophilous and

thermophilous forms mentioned above seem to be relicts of post-Glacial xerothermic (boreal or subboreal) periods.

2. *The fauna of Diptera occurring in the valleys of small rivers is rather peculiar.* A dense cover of leaf-bearing forests prevents wind and direct sun-rays creating conditions favouring the intensive development of many thermophilous and hydrophilous forms. Many of these forms are undoubtedly relicts of warm but damp post-Glacial periods (Atlantic period).

The fauna of large swamps is very peculiar. This affords a supposition that under the conditions of the Leningrad region these species are relicts of cold post-Glacial periods, in particular of the Arctic period.

Very pooı in the number of species but very important for understanding the history of Diptera fauna formation is *an element* which may be (conditionally) *called eastern-siberic.* Ecologically the majority of these forms are connected with damp broad-leaved forests; hence it seems more probable that they are relicts of damp and warm post-Glacial periods. It is suggested that at that period an immigration took place as from south-west so from east.

We are concerned in the question to what extent is the fauna of any region stable in those fractions of a second one man or one generation can observe?

A priori such stability may be supposed not to exist at all. Really, if we compare specific compositions and numerical ratio of species in different years then we shall see that they never repeat themselves: each year has its own faunistic individuality. Apparently the dynamics of the fauna is influenced also by the age of the inhabited territory. It is known that the ages of different parts of the Leningrad region are different. The broad valley of the Neva river and the coast of the Gulf of Finland are younger as compared with other parts of the Leningrad region situated further north and south. The fauna of these regions became free from marine transgressions (Litorina sea) later and thus it is apparently less stable than that of the Leningrad region which had become free from sea earlier.

Such are preliminary results of my investigations of the Diptera in the Leningrad region.

INFLUENCE DES GLACIATIONS PLEISTOCENES SUR LES ORTHOPTERES DES HAUTES ALTITUDES DES APENNINS

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Les Orthoptères des pelouses de l'étage alpin dans les Apennins comprendent nombreuses espèces d'origines differentes qui peuvent être groupées en 3 catégories: A) Espèces autochtones d'origine préquaternaire; B) Néoendémites derivés d'espèces arrivées en Italie pendant le Quarternaire; C) Espèces d'invasion quaternaire qui ne presentent aucune differentiation.

Les espèces autochtones préquaternaires disparaissent brusquement au S du Matese, c'est à dire à la fin de l'Apennin central, par le fait que jusqu'au Pliocène l'Italie méridionale constituait un archipel et n'avait aucun rapport avec le reste de la péninsule.

Les éléments les plus interessants de ce groupe sont 8 espèces aptères sténotopes du genre *Cophopodisma* (présent uniquement dans l'Apennin central et les Pyrénées) qui montrent trois étapes évolutives successives: sur la base de leurs caractères et de leur distribution dans l'Apennin central, on peut admettre que 4 espèces constituaient le peuplement préquaternaire qui, fractionné en populations isolées pendant les derniers interglaciaires, a donné origine aux 8 espèces connues (*C. costai* Targ. Tozz., *C. samnitica* L. G., *C. ebneri* L. G., *C. lucianae* Bacc., *C. baccettii* L. G., *C. acuminata* L. G., *C. fiscellana* L. G., *C. trapezoidalis* L. G.); les 2 dernières espèces, diffuses sur plusieurs reliefs pendant le Würm, montrent aussi une différentiation raciale attribuable à l'isolement survenu au Postglaciaire.

Une histoire évolutive analogue montrent les formes endémiques dérivées d'espèces immigrées dans l'Apennin pendant les premières glaciations pléistocènes: c'est le cas des espèces et des races endémiques du groupe *pedestris* du genre *Podisma* qui dans l'Apennin n'arrive pas au Sud du Gran Sasso. On connait 3 espèces sténotopes, *P. emiliae* Rme (Apennin émilien), *P. silvestrii* Salfi (Monts Sibillini) et *P. goidanichi* Bacc. (Gran Sasso), qui dérivent vraisemblablement de populations pléistocènes de *P. pedestris,* isolées après une

ou plusieurs invasions préwürmiennes; la dernière glaciation a porté sur l'Apennin ligurien et le nord de l'Apennin Tosco-émilien une race W-alpine, la *P. pedestris dechambrei* Leproux, qui a pu donner origine, pendant le Postglacial, à une race nouvelle, *P. p. melisi* Bacc., à l'extremité méridionale de son aire; en réalité dans les Alpes Apuanes existe encore une population avec caractères de transition d'une race à l'autre.

D'autres espèces, immigrées en Italie pendant les dernières glaciations ou seulement pendant le Würm, ne présentent aucune différentiation et sont diffuses plus ou moins profondement vers le sud de la chaîne: il s'agit d'espèces eurosibiriques ou provenantes des monts de l'Europe, desquelles on trouve 12 dans l'Apennin septentrional; de celles-ci, *Omocestus viridulus* (L.), *Bicolorana bicolor* (Phil.) et *Anonconotus apenninigenus* (T.-T.) ne descendent pas au sud de l'Apénnin Tosco-émilien; *Stenobothrus nigromaculatus* (H.-S.), *Decticus verrucivorus*, *Orphania denticauda* (Charp.) L. et *Psophus stridulus* s'arrètent au niveau des Sibillini et de la Majella; *Tettigonia cantans* (Füss.) au Matese; ainsi au Pollino n'arrivent que 4 espèces de ce groupe dont *Myrmeleotettix maculatus* (Thbg.) et le boréo-alpin *Gomphocerus sibiricus* (L.) ne vont pas plus loin. Plus au sud, sur les monts de Calabre subsistent uniquement *Stauroderus scalaris* (F.-W.) et *Stenobothrus lineatus* (Panz.) et seulement cette dernière espèce arrive aussi sur les hauts niveaux des monts de Sicile. Toutes les espèces de ce groupe sont arrivées probablement en Italie une ou plusieurs fois pendant le Riss ou le Würm sans constituer des populations bien isolées pour un temps suffisamment long.

Le Pollino est aussi la montagne la plus méridionale des Appennins, où arrivent encore des endémites quaternaires parmi les plus largement diffus dans la chaîne (*Stenobothrus apenninus* Rme. et *Decticus aprutianus* Capra), où existent les pelouses de l'étage alpin et où l'on trouve les traces d'un glacier würmien.

L'absence ou la rareté, dans l'Apennin méridional, d'élements eualpins immigrés au Pleistocène est un phénomène recent qui remonte à la periode ipsothermique du Postglacial pendant laquelle la limite supérieure des arbres à touché le maximum d'élévation.

COLEOPTERES ENDOGES DES ENVIRONS DE GENEVE

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La région de Genève a été envahie à chaque glaciation par le glacier du Rhône, occupant tout le bassin du Léman, et le glacier de l'Arve, descendant du massif du Mont Blanc. Une épaisseur de glace variant entre 500 et 600 m. a ainsi recouvert Genève et ses environs au cours de la dernière glaciation, qui s'est terminée il y a quelque 10.000 ans.

Holdhaus a montré que les Coléoptères endogés font défaut dans toutes les régions dévastées par les glaces. Or ces insectes sont représentés dans les environs de Genève par dix espèces, *Gynotyphlus perpusillus* Dod., *Typhlocyptus pandellei* Saulcy, *Paraleptusa genavensis* Coiff., *Tychobythinus glabratus* Ryc, *Cephennium argodi* Croiss., *Loricaster testaceus* Muls. Rey, *Langelandia anophthalma* Aubé, *Anommatus diecki* Reitt., *A. duodecimstriatus* Müll. et *Raymondionymus marqueti* Aubé, dont huit sont largement répandues dans la région étudiée. Les *Loricaster* (plus de 400 ex. récoltés en trois ans), *Langelandia* (plus de 1100 ex.), *Annomatus* (plus de 700 ex.) et *Raymondionymus* (env. 350 ex.) sont même très fréquents dans les prélèvements de terre. De plus les Coléoptères endogés ne sont pas seulement bien représentés dans les environs de Genève mais semble-t-il dans toute la région lémanique; *Raymondionymus marqueti* Aubé en particulier a été trouvé près de Vevey et *Eccoptobythus paradoxus* Dev. près de Thonon.

Comment expliquer la présence de ces formes endogées dans une région ayant subi à plusieurs reprises l'action dévastatrice des glaciers? Une introduction accidentelle par l'homme semble exclue, cette faune endogée étant trop largement répandue et variée. Une migration active depuis la région lyonnaise non dévastée par les glaces paraît très problématique, 180 km. en 10.000 ans en remontant la vallée du Rhône étant une distance bien trop grande pour des insectes aussi peu mobiles que les *Gynotyphlus*, *Typhlocyptus* et *Raymondionymus*. Mais il est

probable que les Coléoptères endogés trouvés dans le canton de Genève aient pu se maintenir pendant toutes les glaciations dans les régions de refuge, restées au-dessus du niveau maximum des glaces et au-dessous de la limite minimum des neiges, soit dans les environs de Genève (versant oriental du Jura, parties élevées du Salève et des Voirons), soit dans le bassin de l'Arve (massif du Môle, de la Montagne de Sous-Dine et du Mont La Cha, versant occidental de la chaîne des Aravis); après le retrait des glaces, ils ont gagné la région genevoise par l'une ou l'autre des vallées qui y aboutissent, les crues des cours d'eau ayant certainement facilité dans une grande mesure cette migration. Cette solution est plausible, mais ce n'est encore qu'une hypothèse, la faune endogée des massifs de refuge du Jura et de la Haute-Savoie étant malheureusement totalement inconnue.

Quelle que soit l'origine des espèces trouvées à Genève, cette étude (cf. Mitt. schweiz. ent. Ges. 36, 1963: 313-320) montre qu'une région dévastée par les glaces, même pendant la période wurmienne, peut présenter une véritable faune endogée.

THE GENUS *SCAPHINOTUS* (COLEOPTERA: CARABIDAE) AND THE PLEISTOCENE EPOCH IN SOUTHWESTERN UNITED STATES

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The problem of determining rates of evolution in insects is a difficult one because it is hard to obtain data on the time dimension. Accurately dated fossils provide the best guide, but insect fossils are few, far-between, and usually fragmentary (3). Inferences can be made, however, about rates of change if length of isolation of closely related populations can be determined. In the American Southwest, such inferences can be made for the isolated populations of the genus *Scaphinotus*.

A single species group, the *elevatus* group, of the subgenus *Scaphinotus* occurs in southwestern United States and northwestern Mexico. This group comprises 10 species which can be arranged in three, largely allopatric, subgroups. The species are markedly similar to one another, and on this basis, are likely to be closely related, and hence are likely to have diverged comparatively recently. For the most part, the species have restricted ranges, five being restricted to single mountains. The species are flightless and are confined to coniferous forests. They are found rarely as low as 6000 feet above sea level, and are usually encountered above 7500 feet elevation. The montane coniferous forests and their *Scaphinotus* populations form high altitude communities, isolated from one another by a series of different communities occurring at lower elevations, including the desert or semi-desert vegetation of the lowlands (7).

Because the species are flightless and are unlikely to be spread by accidental means, it follows that their ancestors had to cross the intervening lowlands to produce the now-isolated highland populations. Because the lowlands are at present unsuitable for *Scaphinotus*, it is probable that in the past, climatic conditions were radically different than they are today. Prior to the Pleistocene epoch, palaeobotanical evidence suggests that the lower elevations were occupied by plants of the dry-adapted Madro-Tertiary flora (1). For the Pleistocene, available evidence shows that climate and vegetation have undergone marked changes. During the glacial periods, large lakes occupied a portion of the country which is now desert, suggesting much increased rainfall (4). The pollen record of the glacial stages of the late Pleistocene shows that at low elevations, spruce, fir and Ponderosa pine were prevalent, and plant groups that are at present dominant were, at that time, a much less conspicuous feature of the country (8, 9, 11), again suggesting a more humid cooler, climate. It is likely then, that the pluvial (=glacial) stages of the Pleistocene by causing a shift downward of the life zones, provided suitable habitats in the lowlands for *Scaphinotus*, at least along water courses, and thus allowed inter-montane dispersal to take place.

In a subsequent pluvial stage, dispersal into the lowlands would again be possible, to be followed in turn by another dry interpluvial, and withdrawal to higher elevations. This cycle would explain the known instances of sympatric species, e.g. *elevatus* Fab. and *snowi* Le Conte

in the Sangre de Cristo Mountains of New Mexico. Such a cycle would also explain why some species occur in more than a single mountain range; for example, *snowi*, whose range includes a number of mountains in New Mexico, Arizona, Colorado, and Utah; *vandykei*, occurring on the slopes of the Mogollon escarpment, and in at least three ranges in the sub-Mogollon region. The suggestion here is that each of these species differentiated on a single mountain during an interpluvial, and in a subsequent pluvial period, spread outward to adjacent mountains.

A particularly interesting example of the effect of isolation followed by dispersal and subsequently by isolation, is seen in the case of *Scaphinotus petersi*. This species comprises four subspecies, three occurring on one mountain each, and the fourth occurring on two mountains. One subspecies, *catalinae* Van Dyke, whose geographical range (Santa Catalina Mountains) is more or less central to that of the other subspecies encompasses most of the range of morphological variation of the other three subspecies. The others are strikingly different from one another, and can be distinguished at a glance. In the Santa Catalina Mountains, character combinations are not distributed at random, but rather the high altitude populations, (8500–9000 feet) are most like the subspecies *grahami* Van Dyke, while those from lower elevations (7500–8000 feet) are more like the subspecies *biedermani* Roeschke, and a few specimens are within the range of variation of *petersi*. To explain these facts, it is suggested that, first, the primitive *grahami* became isolated in the Pinaleño Mountains and in the Santa Catalina Mountains. The Santa Catalina population differentiated altitudinally, the specimens with the more derived morphology occurring at lower elevations. During a subsequent pluvial stage, the derived forms spread along the San Pedro River valley, and in post-glacial time, became isolated in the mountain ranges they now occupy; *petersi* in the Pinals; *biedermani* in the Rincon and Huachuca Mountains. The marked differences between these races is thought to be mainly the result of the founder populations consisting of few individuals.

Returning to the general question of evolutionary rates, I suggest that the evolution of *Scaphinotus* in southwestern United States and northwestern Mexico occurred mainly, if not exclusively during Pleistocene time, a span of about 300,000 years (5). In this time span, some isolated populations diverged to species level, then dispersed and differentiated again. In the case of the species *petersi*, under the special circumstance of the partitioning of the total variability among geographical isolates, I suggest that the extant races have become distinct within a span of time including the Wisconsin glacial stage plus post-glacial time. Thus, I suggest that in this group distinct morphological species have been produced in less than 300,000 years, and distinct subspecies in about 35,000 years. These figures are of the same order of magnitude as proposed (2) for species evolution in the subgenus *Cryobius*, but are decidedly greater than the rates of evolution of European boreo-alpine Carabidae (6), and for species isolated in the glacial refugium on southwestern Kodiak Island.

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SOME GLACIATION-ISOLATED POPULATIONS OF NORTH AMERICAN LEPIDOPTERA

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A few examples are presented of populations of Lepidoptera in which speciation, or subspeciation, seems to be correlated with spatial isolations in refugia during Pleistocene glacial or interglacial periods.

Erora Scudder is a small, distinctive genus of Theclinae limited to North and Central, and perhaps northern South America. It may be of ancient boreal origin. *Erora laeta* (W. H. Edwards) ranges along the general Appalachian region from Michigan and Quebec to Tennessee and Kentucky. A closely related population, *E. sanfordi* dos Passos, occurs in thriving colonies in the White Mountains of Arizona and the Mogollon Plateau of New Mexico. *E. quaderna* (Hewitson), perhaps indistinguishable from *sanfordi*, occurs in the high plateau of Central Mexico. Other supposed species, based on a specimen or two each, occur thence southward at considerable elevations. However we may split or lump *laeta*, *sanfordi* and *quaderna*, they obviously represent three closely related but widely isolated populations. *E. laeta* is consistently an inhabitant of upper Transition and, to some degree, lower Canadian Zones, being consistently associated with northern and upland beech (*Fagus*) forest. Fundamentally it is monogeneutic, the adults flying in late Spring. *E. sanfordi* appears similar in zonation and habitat. It seems safe to assume that connections of a suitable habitat must have existed (but not necessarily synchronously) between the southern Appalachians and the Southwest, and between the Southwest and the Mexican Plateau, where today there are highly arid, hot plains and deserts. Very likely the Ozark Plateau of Missouri was involved in the first of these connections. Estimates by various workers of the altitudinal extent of Pleistocene Life Zones in the Southwest and thence to the Mexican Plateau differ widely (e.g. Antevs 1954); but the undoubted existence of spruce through central Mexico at 7,000 feet and its presence in the Valley of Mexico seem conclusive evidence of at least an upper Transition Zone connection between the New Mexico mountains and the Mexican Plateau. It would be remarkably interesting if an *Erora* population could be found and studied in the Ozarks, where one may well exist.

In the genus *Crambus* Fabricius (Pyralidae) a group of species now limited to high Transition and lower Canadian Zone meadows in New Mexico and Arizona show correlations like that of *E. sanfordi* and *quaderna*. In *C. sargentellus* Klots there is little, if any, difference between the New Mexican and Mexican specimens. However, in *C. angustexon* Blesczynski there are slight but constant differences in both pattern and male genitalia between the populations of New Mexico and Arizona and of Central Mexico.

A considerable number of species appears to have survived the Pleistocene glaciations solely in the Great Basin area between the Rocky Mountains and the Sierras, doubtless moving down into the lower levels of the Basin as cooling and mountain glaciations increased. For example, the nymphalid butterfly *Boloria kriemhild* (Strecker) is now limited to Canadian zone forest meadows around the eastern and northern edges of the Basin, never east of the continental divide. Some of its Utah populations differ slightly from the more northern ones.

A continent-wide crambine, *Tehama bonifatella* (Hulst), has a most striking discontinuous distribution. In eastern North America it occurs in Greenland, Labrador, Newfoundland and Nova Scotia (where it is very rare and local). In the West it is common and widespread in the Rocky Mountains south into New Mexico, and west of the Great Basin from British Columbia south through most of California. The western populations also show signs of adaptation to considerably lower zonal levels, occurring from about mid-Canadian Zone well down into mid-Sonoran (=Austral). It has been taken at Bandelier National Monument, N.M. in a hot xeric canyon bottom. In California it is, in fact, something of a pest in lawns almost down to sea level.

It seems reasonable to suppose that during the Pleistocene glaciations *bonifatella* survived in at least two refugia, one in the extreme East, the other (or others) in the West, most probably in the Great Basin region. The failure of the eastern population to survive in most of the potential continental area is noteworthy. In the West the dissimilarity of the Rocky Mountain

and California populations suggests two different refugia, the more western one west of the Sierras.

With recognition of the true sphagnum bog as fundamentally a northern Canadian, or even Hudsonian, Life Zone habitat, the isolated southern bogs left behind the glacial recessions appear as relic areas just as truly as mountaintops above timberline. Many bog-obligate, relic populations of insects are known, and doubtless many others will be recognized. *Boloria eunomia* (Esper) (Nymphalidae) and *B. frigga* (Thunberg); and *Bactra lanceolana* (Haworth) (Olethreutidae) are but three of many species that have survived in widespread, isolated bog colonies in North America and also occur widely in the Palaearctic Region.

More attention should be given to the importance of Florida as an island or archipelago refugium, cut off the mainland during Pleistocene interglacials. There is considerable difference of opinion among authorities (2, 5, 6) as to the various levels of the ocean during the Pleistocene. However, there seems no doubt that, probably more than once, the central "highlands" of peninsular Florida became an isolated refugium for many species.

The nominate subspecies of the "hairstreak" *Strymon falacer* (Godart) (Lycaenidae) occurs today in central peninsular Florida. It has extremely long tails on the hindwings, considerable development of orange-red on the under sides of the wings, and often an orange patch on the upper side of the hindwings. The widely ranging mainland subspecies *S.f. calanus* (Huebner) occurs from Georgia westward and northward into Texas, Oklahoma, Manitoba and Quebec. It has much shorter tails, much less orange-red on the under sides of the wings, and no orange patch on the upper side of the hind wings. In a blend zone in northern Florida and southern, coastal plain Georgia occurs a rather variable hybrid population with tails almost as long as those of the central Florida population, but having essentially the colors of the northern one. There seems little doubt that *S.f. falacer* represents a peninsular Florida refugium population which did not, however, evolve full specific status. It may be noted that there is also a fairly distinctive "subspecies" of *falacer*, e.g. *godarti* Field, in the Rocky Mountains area, isolated by the arid Great Plains.

Finally, the pierid Falcate Orange Tip, *Anthocaris midea* (Huebner) shows much the same thing. A very limited population along the shore regions (including the "sea islands") of Georgia and South Carolina has the orange apical patch of the male forewing very extensive. Very rarely, specimens of this form appear in the coastal plain north to Washington, D.C. Immediately inland and in the piedmont and westward into Texas and northward into Connecticut and Missouri, the population has a consistently reduced orange patch. Most curiously, however, near the northwestern limit of the species in Missouri, extensive orange patches again appear in local populations, but merely as an extreme color form in a highly variable population all flying together. While the southeastern Coastal Plain "large patch" can be regarded as evidence of some differentiated evolution during a Pleistocene interglacial isolation, perhaps in isolated Florida, the Missouri "large patch" is something entirely independent.

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INSECT DISTRIBUTIONS THAT INCLUDE THE SOUTH TEMPERATE ZONE

ON THE REAL NATURE OF TRANSANTARCTIC RELATIONSHIPS

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The paper, based on an extensive material of chironomid midges collected by the author in the mountain streams of temperate South America, Tasmania, New Zealand and East Australia, dealt with the relationships of austral bicentric and tricentric groups. A critical study of decisive synapomorphic characters demonstrates that the relationships are orderly throughout, thus forming fixed patterns giving insight into the history of the old antarctic element of southern lands.

THE INFLUENCE OF PLEISTOCENE GLACIATIONS ON THE DISTRIBUTION OF SOME TENEBRIONIDAE (COLEOPTERA) IN NEW ZEALAND

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The highest parts of New Zealand were substantially glaciated during Pleistocene times. The Southern Alps supported large icefields, and valley glaciers joined on the lowlands to the west to form a continuous piedmont glacier. There were a few other centres of relatively minor glaciation (1). The regional snowline was depressed at least 3,500 feet during the later glaciations. Mean summer temperature was about 6°C lower than at present (2). Forest was almost eliminated from the eastern South Island, but there may have been forest refuges in a few sheltered localities. Subalpine grassland and scrub extended to present sea-level in the south of the North Island, as shown by studies of fossil pollen.

The tenebrionid genus *Cilibe* comprises 20 known species of medium to large flightless beetles with soil-inhabiting larvae. I believe that eight of these probably speciated during the Pleistocene. In *C. humeralis* isolation was due to a high interglacial sea-level, but most of the others seem to have been isolated originally in limited areas by severe periglacial conditions during glaciations. *C. opacula* has two morphologically distinct populations (subspecies) isolated on islands in the north which were connected with the mainland during the last glaciation. The nearest mainland population now exists about 80 miles to the south. The only simple explanation for this situation is that the isolated island populations have evolved their distinctive characters in postglacial times. Several species show substantial gaps in their ranges, but there is no apparent reason why they should not be able to exist there. These gaps probably reflect extinction of populations duiing the last glaciation when the species in the South Island were confined presumably to a few favoured refuges (e.g. *C. elongata*, *C. rugosa*). Some species show complex patterns of geographical variation which make more sense if populations isolated during the last glaciation have since come together again. Four species of *Cilibe* have a predominantly subalpine distribution today, which suggests adaptation to periglacial climate during glaciations.

There are 16 species of *Cilibe* which occur in the South Island, and 13 of these are confined to that island. In the genus *Pheloneis* all but two of the 31 described "species" are confined to the South Island. The latter genus occurs in the dense wet forests of Fiordland and Westland, which are apparently too moist for *Cilibe*. Most of the other large flightless Tenebrionidae are confined to the South Island, although there are thiee genera restricted to the far north of the North Island; each containing only one or two species.

Thus, the vast majority of the large flightless Tenebrionidae of New Zealand are confined to the colder South Island. Apparently stenothermal warmth-loving species were eliminated or survived only in the far north during glaciations, and the remainder of the fauna became adapted to cool or cold climatic conditions.

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FAUNAL RELATIONSHIPS OF THE MORE SOUTHERN SUBANTARCTIC ISLANDS (MACQUARIE, CAMPBELL, AUCKLANDS, HEARD, SOUTH GEORGIA)

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The subantarctic islands, widely scattered around the Antarctic continent, mostly between 48° and 55° South Latitude, have diverse faunas. There are certain characteristics in common, but great differences between some. With islands of similar size and latitude, the faunal differences suggest quite different histories. In the past, contrasts in representation might have been attributed to unequal sampling. Now, however, it seems clear that striking differences do exist.

The islands here discussed include five of the seven most southern isles or groups north of 60° S. Lat. and excluding South America. They are listed here both by latitude and by longitude (south to north; west to east):

Macquarie	54°30′ S. Lat.	South Georgia	36° W. Long.
South Georgia	54° S. Lat.	Heard	74° E. Long.
Heard	53° S. Lat.	Macquarie	158° E. Long.
Campbell	52°30′ S. Lat.	Aucklands	165° E. Long.
Aucklands	50°30′ S. Lat.	Campbell	169° E. Long.

From the above it is seen that the latitudinal range is slight, but the isles are in part very widely separated. South Georgia and Heard are about 110° apart, and Heard and Macquarie about 84° apart. Although Macquarie is almost as close to the Aucklands as Campbell is, the fauna of Macquarie is much poorer than, and rather different from, those of Campbell and the Aucklands. Likewise, South Georgia and Heard both appear to be much poorer than Macquarie.

Table 1

Faunal representation on southern subantarctic islands: numbers of families, by orders

	(Antarctica)	*South Georgia*	*Heard*	*Macquarie*	*Campbell*	*Aucklands*
Collembola	3	3	2	5	6	6
Orthoptera	—	—	—	—	1	2
Plecoptera	—	—	—	—	1	1
Psocoptera	—	—	—	1	3	3?
Phthiraptera	3	3	3?	3	3	3
Odonata	—	—	—	—	—	1
Thysanoptera	—	1	—	1	1	1?
Hemiptera	—	—	—	1	2	3
Trichoptera	—	—	—	—	1	1
Lepidoptera	—	1?	1	1	7	8
Coleoptera	—	3	2	1	10	12
Diptera	1	6	4	9	30	31
Siphonaptera	1	2?	2	3	3	3?
Hymenoptera	—	—	—	2	6	8
Total families Insecta	8	19	14	27	74	83
Total species Insecta	36	50+	25+	65	258	336
Total species Arachnida, myriopods, Insecta	56	70+	31+	103	354	453+
Genera in common	8	6+	7+	16	70	

General faunal representation on the islands is indicated in Table 1. South Georgia, Heard and Macquarie do not have a great many elements in common. South Georgia's relationships are largely with the Falklands, southernmost South America and the Antarctic Peninsula—S. Shetlands area. Heard's relationships are largely with Kerguelen, and

Campbell and Aucklands' strongly New Zealand. Macquarie has ıelatively a higher percentage of forms in common with Heard than with Campbell or Aucklands.

In general, faunal elements are distributed clockwise about the Antarctic continent. Many must have been carried by air or sea currents, or by birds, all more or less going in this direction. Probably air dispersal has been most important for South Georgia, Heard and Macquarie, at least. Campbell and the Aucklands may have a number of relicts from an earlier more extensive New Zealand area land mass. Insects trapped at sea in this area and off southern South America are in general of types represented on subantarctic islands.

Among characteristics of the subantarctic fauna are extreme disharmony of representation, general scarcity of predators and parasites of insects, dominance of scavengers and vertebrate parasites, and prevalence of wing reduction. Percentages of wing reduction or wing loss among the normally winged groups is approximately as follows:

(Antarctica	50)	Macquarie	68
Heard	100	Campbell	40
South Georgia	80	Aucklands	35

Some brachypterous genera, like *Halyrytis* of the Chironomidae, occur in Tierra del Fuego-Kerguelen-Macquarie, while others, like the brachypterous moths and various coelopid and other flies, are limited to adjacent isles, as for instance Crozet-Kerguelen-Heard, oı Campbell-Aucklands. As examples of erratic occurrence of various elements may be cited the presence of Dytiscidae on South Georgia only, weevils on all the isles except South Georgia and Macquarie, Staphylinidae on all but Heard, Dolichopodidae on Macquarie-Campbell-Aucklands, and many families only on Campbell-Aucklands.

The following figures indicate the numbers of families having their southernmost limits on the various respective islands:

(Antarctica	8)	Heard	5
Macquarie	18	Campbell	26
South Georgia	6	Aucklands	20+

THE PSYCHODID FLIES OF THE SOUTH TEMPERATE ZONE

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Most of the Australasian species of Psychodidae are contained in the genera *Psychoda Pericoma* and *Telmatoscopus*. With the exception of *Pericoma*, the relationships of this fauna is closest to the Oriental and Palaearctic Regions. *Pericoma* seems most closely related to South American species. One autochthonous genus, *Atrichobrunettia*, is found here. Two highly modified species of *Psychoda* are on the subantarctic islands.

The dominant genera in South America are *Psychoda*, *Pericoma*, *Trichomyia* and *Phlebotomus*. Four autochthonous genera are present and many distinct species which produces a highly characteristic and distinctive fauna of psychodids. The Neotropical species are poorly known and, other than some Australasian relationships, affinities of South America are difficult to determine.

African psychodids largely belong to the genera *Psychoda*, *Telmatoscopus*, and *Phlebotomus; Pericoma* is apparently replaced by *Clytocerus*. There are no autochthonous genera and the closest relationships are with the Holarctic Region. There is no evidence of direct contact with the Australasian or Neotropical Regions.

There are only two psychodid groups which suggest Antarctic migration routes. *Pericoma* has a distinctive subgroup which is almost entirely limited to Australia, New Zealand and South America with minor representation in the north. The tropics seem to be a barrier as the genus is scarce or absent there. It would appear that this subgroup of *Pericoma* may have moved directly between South America and Australasia. *Nemoneura* also suggests Antarctic connections in possessing two Patagonian and two (undescribed) New Zealand species.

In the south temperate zone, the genus *Psychoda* is a dominant genus in all areas. *Pericoma* is dominant in Australasia and South America, but not in Africa; *Telmatoscopus* in Australasia and Afiica, but not South America; and *Trichomyia* only in South America. The genus *Clytocerus* replaces *Pericoma* in Africa, but is poorly represented elsewhere. *Phlebotomus* has many species in South America and Africa, but is rather scarce in Australia and absent in New Zealand.

It is concluded that the greatest part of the south temperate Psychodidae fauna has been derived from adjacent land masses to the north. Most of the faunas of Australasia, South America and Africa differ markedly and do not suggest a common origin. Only in two groups limited to Australasia and South America are there suggestions of Antarctic interchange between these areas.

VERBREITUNGSGESCHICHTE DER GRIPOPTERYGIDEN (PLECOPTERA) IN DER SÜDLICHEN HEMISPHÄRE

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In seiner grundsätzlich bedeutungsvollen Studie über die Dipterenfauna Neuseelands hat sich Hennig 1960 kritisch mit der Frage auseinandergesetzt, inwieweit das tiergeographische Phänomen der amphinotischen Verbreitung (Australien, Neu-Seeland, Süd-Amerika) als Argument für eine frühere Existenz direkter Verbindungswege (via Antarctica) von Bedeutung ist. Mit Recht weist er darauf hin, daß der bloße Nachweis der Existenz von AS-Gruppen,

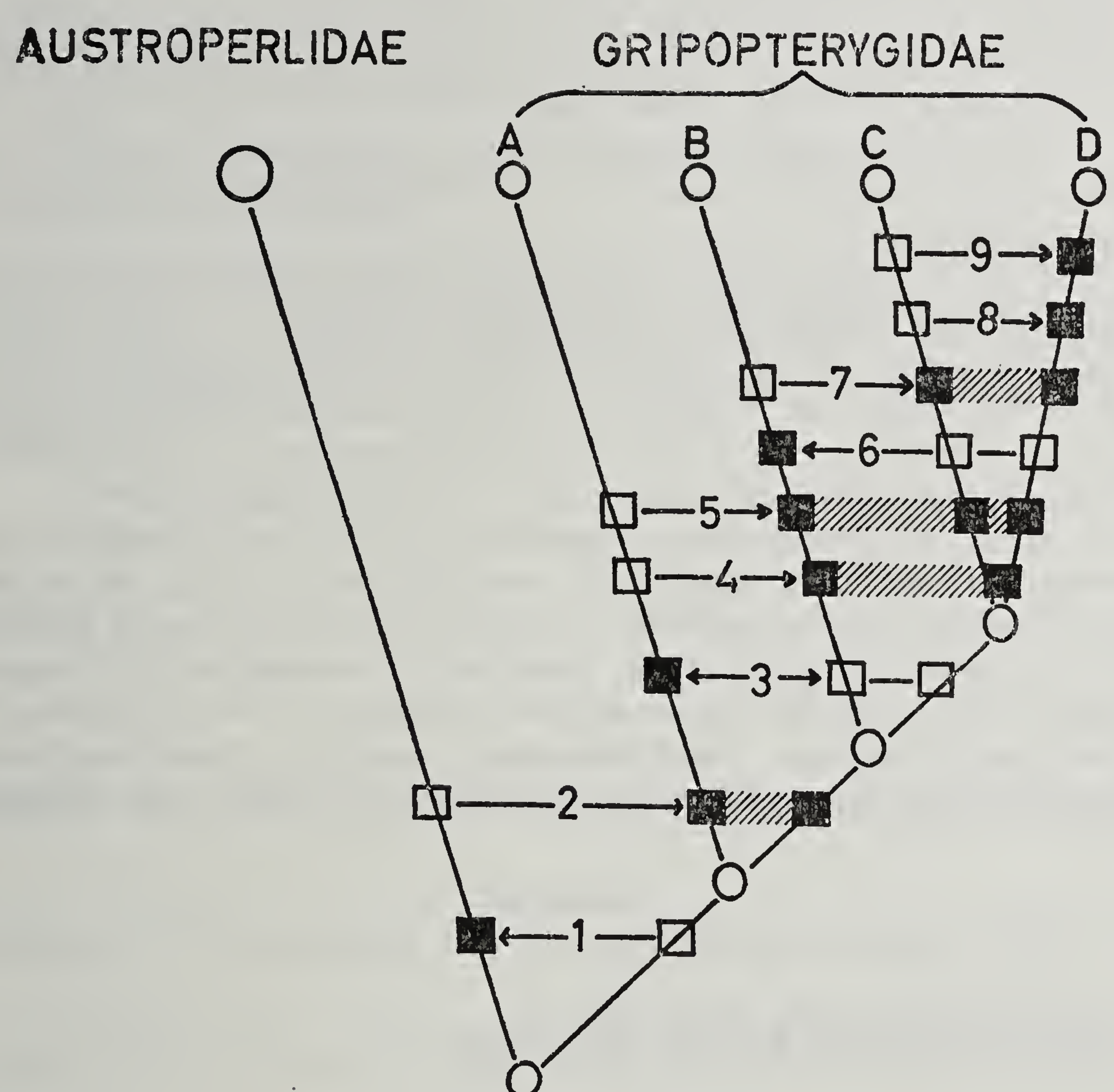

Abb. 1. Argumentationsschema für die Verwandtschaft der vier Unterfamilien der Gripopterygidae und der Familie Austroperlidae (Synapomorphie-Schema nach Hennig 1957). Die einzelnen Unterfamilien der Gripopterygidae sind durch Buchstaben dargestellt; es bedeuten A: Gripopteryginae, B: Paragripopteryginae, C: Leptoperlinae, D: Antarctoperlinae. (Die nähere Bezeichnung der Merkmale 1-9 siehe im Text).

also solcher mit ausschließlich australisch-südamerikanischer Verbreitung, noch keine Notwendigkeit für die Annahme früherer transantarktischer Landverbindung darstellt, da die Möglichkeit einer Einwanderung dieser Gruppe aus dem Norden nicht ausgeschlossen werden kann.

Erst die Frage nach der nächstverwandten Schwestergruppe, d. h. die Betrachtung der systematisch-phylogenetischen Nachbarschaft einer solchen AS-Gruppe, kann zu einem solchen Beweise führen.: "Von sehr triftigen Gründen für die Annahme einer früheren antarktischen Landverbindung könnte man sprechen, wenn sich ganze Komplexe nahe miteinander verwandter AS-Gruppen finden lassen sollten" (Hennig l.c. p. 297). Da für alle von ihm untersuchten amphinotischen Dipterengruppen die nächstverwandten Schwestergruppen in der Nordhemisphäre zu finden sind, erfüllt keine von ihnen die gestellten Bedingungen; Hennig kommt daher zu dem Schluß, daß die Dipteren für den Nachweis einer transantarktischen Landverbindung ungeeignet erscheinen und daß ein solcher Nachweis in der Tiergeographie bisher aussteht.

Bei den Plecopteren ist die Situation wesentlich günstiger, da sie geologisch bedeutend älter sind (mit Sicherheit seit dem Perm bekannt), geringe Ausbreitungsenergie besitzen (viele flugunfähige Formen) und weitgehend auf die gemäßigten Breiten mit kühlen Fließgewässern beschränkt sind (die Tropen stellen ein Verbreitungshindernis dar).

Fast alle Plecopterenfamilien sind daher auf die gemäßigten Breiten der nördlichen oder der südlichen Hemisphäre beschränkt; die Mehrzahl der plesiomorphen Familien sind AS-Gruppen im Sinne Hennigs. Nachdem in den letzten Jahren die konsequent-phylogenetische Systematik dieser südhemisphärischen Familie in großem Umfang geklärt werden konnte, wird es nunmehr möglich, in der Familie der Gripopterygiden eine Gruppe vorzuführen, die die von Hennig gestellten Bedingungen in vollem Umfang erfüllt.

Gripopterygiden sind in Südamerika, Australien (mit Tasmanien) und Neuseeland (mit subantarktischen Inseln Campbell und Auckland) verbreitet, und zwar nach unserer heutigen, recht genauen Kenntnis in 88 Arten. Eine eingehende Revision dieser Gruppe (3) zeigt, daß sich diese Arten auf 30 Gattungen verteilen, welche sich ihrerseits zwanglos zu vier Unterfamilien gruppieren, von denen sich jede durch Synapomorphien als natürliche, konsequent-phylogenetische Einheit erweist.

In Abb. 1 ist (nach Hennig 1957) ein Synapomorphie-Schema für die Gripopterygidae und die nächstverwandte Gruppe der Austroperlidae entworfen. Es sind dabei jeweils die apomorphe (schwarz) und die plesiomorphe (weiß) Ausprägungsstufe eines Merkmales angegeben, und zwar bezogen auf 1: Cerci und Paraprocten als Hilfskiemen, 2: Analkiemen, 3: Tergit XI (♂), 4: Pleurite am Tg. X (♂), 5: Costal-Queradern, 6: Verschmelzung $RS_1 + R$, 7: Körpergröße, 8: Verschmelzung Pleurite X (♂), 9: Verkürzung der Cerci.

Jede der in Abb. 1 dargestellten vier Unterfamilien der Gripopterygiden und ebenso die Familie Austroperlidae ist tiergeographisch eine AS-Gruppe, d.h. sie ist in Australien (Neuseeland) und in Südamerika verbreitet. Damit sind die von Hennig geforderten Bedingungen erfüllt, ein ganzer Komplex nahe miteinander verwandter AS-Gruppen ist nachgewiesen. Daraus ergibt sich die zwingende Notwendigkeit, für die Entstehung der Familie Gripopterygidae eine ehemalige Landverbindung zwischen Australien-Neuseeland und Südamerika anzunehmen, wie sie z.B. in der Epeirophorese-Theorie von Wegener postuliert wurde.

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THE DISTRIBUTION OF THE ULOPINAE (HOMOPTERA, CICADELLIDAE)

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The principal problems associated with the distribution of exclusively southern hemisphere insects would seem to be the following:

(*a*) Were they formerly also widespread in the northern hemisphere?

(*b*) If always restricted to the southern hemisphere, by what means (over land surfaces, or by adventitious transport) were they enabled to become established in land areas which are now widely separated?

(*c*) If terrestrial distribution is a necessary explanation, what were the geological factors that made this possible?

(*d*) When did these factors operate?

Three of these questions were discussed in the light of the present known distribution of the Ulopinae, a subfamily of the Cicadellidae. One question (*c*), lies outside the scope of biological inquiry.

The Ulopinae have four recognised tribes. The Ulopini, are of almost universal occurrence, including New Zealand, but have not been recorded from the Western Hemisphere.

The Megophthalmini have been recorded from Europe, Western North America, Juan Fernandez and East African mountains.

The Cephalelini, which have probably been derived from the Ulopini, from South Africa, Australia and New Zealand and the Myerslopiini from Madagascar, New Zealand and Chile.

The small size of these insects, the frequency of their occurrence in a flightless condition and their specialised environmental requirements preclude their distribution by adventitious means.

Their morphological characteristics and their distributional association with other relict organisms suggests a Mesozoic origin.

Reasons were given for supposing that the Ulopinae, as a whole, became differentiated in the southern hemisphere not later than Jurassic times, that their present pattern of distribution requires dispersal over land surfaces and that the occurrence of a few representatives of the Ulopini and Megophthalinini in the northern hemisphere is associated with post-Eocene dispersal factors.

AFRICA AND THE ATLANTIC AND INDIAN OCEAN ISLANDS

DIE INSEKTENFAUNA DER MAKARONESISCHEN INSELN

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Der englische Forscher und Entomologe Vernon Wollaston besuchte die mittelatlantischen Inseln vor ungefähr einem Jahrhundert. In diesem Jahr sind es genau hundert Jahre, seitdem er seine Zusammenstellung über die Käferfauna der Kanaren herausgab. Schon vordem waren von ihm Arbeiten über die Fauna der Madeira-Inseln erschienen; einige Jahre später

veröffentlichte er die Ergebnisse seiner Untersuchungen über die Käferfauna der Kapverdischen Inseln.

Im Laufe der seither vergangenen hundert Jahre, besonders während der letzten Jahrzehnte, ist auf den makaronesischen oder mittelatlantischen Inseln fleissig gesammelt worden. Noch immer aber sind die Forschungen Wollastons unbedingt die wichtigsten auf diesem Gebiet.

Nicht nur auf Grund meiner eigenen Einsammlungen auf den genannten Inseln, sondern auch gestützt auf die Sammelergebnisse anderer sowie auf das Schrifttum, habe ich im Laufe der Jahre versucht, das von den makaronesischen Inseln vorliegende Material meinesteils zu bearbeiten und im Druck herauszugeben. Die Mitarbeiter sind zahlreich gewesen.

Ich will zunächst einiges über die mir persönlich etwas vertrautere Koleopteren- und Hemipterenfauna der Kanarischen Inseln berichten. Wollaston notierte auf diesen Inseln etwa tausend Käferarten. Spätere Forschungen haben die Zahl auf nahezu 1400 erhöht. Bekanntlich ist eine Inselfauna vor allem durch die Anzahl der endemischen Arten charakterisiert. Wie hoch diese Anzahl innerhalb der ganzen Gruppe der Koleopteren ist, dürfte wohl schwer zu sagen sein; jedenfalls unter den Curculioniden beträgt ihr Anteil 78%, unter den Tenebrioniden 76% und unter den Scolytiden fast 60% sämtlicher kanarischen Arten der betreffenden Gruppe.

Hinsichtlich der Verbreitungsverhältnisse der endemischen Arten auf den Kanarischen Inseln wird man u.a. auf einen wichtigen Zug aufmerksam. Die östlichen sog. Purpurarien (Fuerteventura, Lanzarote und benachbarte Kleininseln) beherbergen oft eine gemeinsame, spezielle Art aus einer innerhalb der ganzen Inselgruppe durch mehrere Arten vertretenen Gruppe. Diese Art fehlt auf den westlichen und mittleren Inseln, die in nicht wenigen Fällen jede für sich ihre eigene Art oder ihre eigenen Arten haben. Kommt eine Art auf mehreren Inseln gemeinsam vor, so handelt es sich um einander genäherte Inseln. Nicht nur die abweichenden ökologischen Verhältnisse, sondern auch die Paläogeographie der wüstenartigen Purpurarien bedingen den scharfen Unterschied der Fauna den übrigen Kanaren gegenüber. Kennzeichnend für die ersten ist das Fehlen zahlreicher typischen kanarischen Arten und Gattungen. Dagegen konstatiert man eine grössere Ähnlichkeit der Purpurarien-Fauna mit dem angrenzenden Kontinent. Alles das deutet auf einen näheren Zusammenhang (eine spätere Landverbindung) zwischen den Purpurarien und dem Festland in vergangener Zeit hin.

Nicht wenige Insekten, u.a. Koleopteren, dürften auf den Kanarischen Inseln vom Menschen eingeführt sein. Sie stammen hauptsächlich aus dem Mittelmeergebiet, ein Teil wohl aus der Neuen Welt.

Es gibt jedoch eine Anzahl Käfer, in bezug auf welche man behaupten kann, dass sie ihre umfassende rezente kontinentale Verbreitung und ihr anschliessendes Vorkommen auf den makaronesischen Inseln nicht dem Menschen zu verdanken haben. Das gilt z.B. für gewisse der kanarischen und zum Teil auch der madeirischen und kapverdischen Fauna angehörende Tenebrioniden. Es handelt sich um flügellose und ähnlich vielen Tenebrioniden an den Erdboden gebundene Arten, und zwar sind es einerseits Uferbewohner auf salinem Grunde oder auf Stranddünen, anderseits wieder Arten, die nicht an die Küste gebunden sind. Den ersten begegnet man, ausser auf den Inseln, noch an der nordwestafrikanischen Küste, an der Mittelmeerküste und auf Binnenlandsalinen. Geeignete Biotope finden sie meistenteils auf den östlichen Kanarischen Inseln. Man kann sich zwar denken, dass sie mit dem Wasser und den Winden von einer Küste zu der anderen gelangt sind, glaublich ist es aber kaum. Das ausgedehnte kontinentale Binnenlandvorkommen der letzteren wiederum und ihr allgemeines Auftreten auf nicht küstennahen Biotopen auf den meisten oder jedenfalls auf vielen der makaronesischen Inseln scheinen weitgehend die Auffassung zu stützen, dass eine Landverbindung zwischen den hier in Rede stehenden Inselgruppen und dem angrenzenden Festland einmal bestanden hat.

Auch wenn zwar die Fauna des Madeira-Archipels einige für diese Inselgruppe endemische Gattungen umfasst (von Carabiden *Elliptosoma* und *Eurygnathus*, von Tenebrioniden *Hadrus* und *Ellipsocoris*), gehören die madeirischen und kanarischen Endemiten mit wenigen Ausnahmen denselben Gattungen (*Calathus*, *Tarphius*, *Laparocerus*, *Lichenophagus* usw.) zu. Für beide Inselgruppen gemeinsame Arten (nordmakaronesische Endemiten) gibt es unter den Koleop-

teren nur wenig, unter den Hemipteren sind sie dagegen recht zahlreich. Diese Paläoendemiten sind in Waldgebiet, d.h. auf den westlichen und mittleren Kanaren und der Hauptinsel von Madeira beheimatet. Wie das obengenannte Vorkommen gemeinsamer Arten in der Madeira- und der kanarischen Gruppe, weist die Ahnlichkeit der Waldfaunen in den westlichen Teilen dieser Inselgruppen auf einen nahen Zusammenhang zwischen ihnen, der indessen nicht eine direkte Landverbindung gewesen zu sein braucht, sondern eine Verbindung zwischen jeder von ihnen und einem kontinentalen Gebiet. Dass die beiden Inselgruppen ihre Fauna auf verschiedenen Wegen empfangen haben, wird dadurch erwiesen, dass die nicht endemischen Hemipteren der Madeira-Inseln grösstenteils eine eurosibirische oder europäische Verbreitung aufweisen, während die meisten von den Kanaren bekannten Hemipteren mediteri an sind.

Und dann noch einige Worte über die Kapverdischen Inseln. Wollastons Auffassung über eine (in grossen Zügen) gleichartige Fauna durch die ganze makaronesische Inselwelt beruhte teilweise darauf, dass ein auffälliges Tier, die Tenebrionide *Hegeter tristis*, auf Madeira sowohl wie auf den Kanaren, den Kapverdischen Inseln und den Azoren allgemein zu finden ist (und neuerdings auch von der nordafrikanischen Küste vorliegt). Dieser Käfer stammt sicherlich von den Kanarischen Inseln, er hat sich aber zu einer anthropochoren Art entwickelt und vertritt in der indigenen makaronesischen Fauna in Wirklichkeit so gut wie den einzigen gemeinsamen Zug zwischen den Kapverdischen und den nördlichen Inseln. Im übrigen sind die Insektenfaunen auf den nordmakaronesischen Inseln und den Kapverdischen Inseln durchaus verschieden. Allmakaronesische Endemiten fehlen ganz. Keine einzige der in so viele Arten aufgespaltenen Käfergattungen der Nordmakaronesen (z.B. *Calathus*, *Tarphius*, *Hegeter* mit Ausnahme des erwähnten *H. tristis*, *Laparocerus*, *Lichenophagus*) ist auf den Kapverdischen Inseln vertreten. Und umgekehrt, die kapverischen Gattungen *Oxycara*, *Trichopodus* (*Tenebrionidae*), *Dinas* (*Curculionidae*) usw. sind auf den nördlichen Inseln nicht vertreten.

Wollaston teilt von den Kapverdischen Inseln 270 Käferarten mit. Gemäss späteren, heute noch grösstenteils unveröffentlichten Sammelergebnissen beträgt die Zahl heute schon mehr als 400. Über den Anteil der Endemiten findet man nur wenige aktuelle Angaben. Von den im ganzen 57 festgestellten Arten und Unterarten der Tenebrioniden sind 32 Arten endemisch, für die Carabiden lauten die entsprechenden Zahlen auf 58 und 18. Dr. Mateu hat in einer noch nicht fertiggedruckten Arbeit unter den Carabiden 28 afrikanische (äthiopische), 9 atlantisch-mediterrane und 3 mehr oder minder kosmopolitische Arten unterschieden. Von den Endemiten sind nach ihm 10 einem älteren paläarktischen Typ zuzählende sog. Paläoendemiten, 8 sind afrikanische Neoendemiten. Mateu teilt also in betreff der Carabiden die von mir in bezug auf die Hemipteren ausgesprochene Auffassung: Es gibt ein älteres paläarktisches Element von hauptsächlich in grösseren Höhen lebenden Formen. Die äthiopischen Hemipteren (Heteroptera und Homoptera Cicadina) machen 40% der Endemiten aus und sind vor allem im Bereich der Kultur und in Steppengebieten zu finden, wo sie gleich den übrigen Vertretern der äthiopischen Fauna so individuenreich auftreten, dass man leicht zu der Vorstellung gelangt, die insulare kapverdische Fauna sei ausgeprägt äthiopisch.

Die Endemiten sind auf den Kapverdischen Inseln prozentisch nicht so zahlreich wie auf den Kanaren. Ihr Vorkommen—dies gilt besonders den flügellosen Formen unter den Tenebrioniden und Curculioniden—ist dort auf eine einzelne oder auf vereinzelte einander genäherte Inseln beschränkt (z.B. *Oxycara*, *Trichopodus*, *Ammidium*, *Dinas*), Die weiteste Verbreitung innerhalb der Inselgruppe weisen die vorgenannten kontinentalen, ebenfalls ungeflügelten Tenebrioniden auf, deren Vorkommen, wie früher schon erwähnt wurde, eine Stütze für die Auffassung bildet, dass es einst Landverbindung zwischen den makaronesischen Inselgruppen und Afrika-Europa gegeben hat.

DAS ENTSTEHUNGSPROBLEM DER MAKARONESISCHEN INSELN UND DESSEN BEDEUTUNG FÜR DIE ARTENTSTEHUNG

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Die makaronesischen Inseln umfassen die Inselgruppen der Kanaren, Salvages, Madeiren, Azoren und Kapverden. Die Madeiren und Kanaren sind sehr artenreich und bieten die besten Untersuchungsmöglichkeiten.

Die Insektenfauna der Kanaren und Madeiren ist überwiegend mediterran. Allgemein bekannt ist die hohe Durchschnittszahl endemischer Formen (nach Peyerimhoff 20% der Gattungen und sicherlich 50% der Arten). Der Prozentsatz der Endemismen schwankt bei den einzelnen Familien oder Gattungen erheblich. Die unterschiedlichen Prozentsätze beruhen auf der Tatsache, dass einige Familien besser untersucht worden sind als andere. Der Prozentsatz der Endemismen wird aber unterschiedlich bleiben. Der Grund hierfür dürfte in ökologischen oder tiergeografischen Faktoren zu suchen sein. Bei gut untersuchten Gruppen kommt ein weiterer Faktor hinzu: die unterschiedlichen Entwicklungsgeschwindigkeiten. Der hohe Durchschnittsprozentsatz deutet auf ein hohes Alter der makaronesichen Inseln.

Die Inseln haben eine fast komplette mediterrane Fauna. Eine so vollständige Fauna lässt nur den Schluss zu, dass es früher Landverbindungen gegeben haben muss.

Die Geologie kommt zu anderen Resultaten. Nach Krejci-Graf entstand der Sockel der makaronesischen Inseln durch vulkano-tektonischen Zusammenschub geschichteter Vulkangesteine.

Scharf umrissen lautet somit das Entstehungsproblem der makaronesischen Inseln, dass sie für die Zoologie kontinental und für die Geologie ozeanisch sind.

Da aufwärts gerichtete Vertikalbewegungen nachweisbar sind, ist es nicht auszuschliessen, dass dann auch abwärts gerichtete Vertikalbewegungen existiert haben. Ein innerhalb langer Perioden, Sich-Heben und -Senken grosser Erdschollen lässt die Möglichkeit offen, dass immer wieder Verbindungen der Inseln untereinander oder mit dem Kontinent bestanden haben.

Die bathymetrische Karte zeigt, dass die eben geschilderte Möglichkeit der Inselentstehung reell ist. Der Graben zwischen den Madeiren und den Kanaren scheint der älteste Bruch zu sein, da die Faunen der Madeiren und der Kanaren untereinander viel unterschiedlicher sind, als die Faunen zweier Inseln der gleichen Gruppe untereinander.

Diese Ansichten finden eine Stütze bei Hausen, der es für möglich hält, dass die eigentliche Grenze des afrikanischen Sial-Blocks westlich von La Palma liegt. Hausen hält weiterhin Zusammenhänge zwischen der Orogonese in Marokko und vulkano-tektonische Unruhe im Randgebiet des Sial-Blocks für möglich. Diese Unruhe wäre dann die eigentliche Ursache der Nesogenese. Auf den Bruchstücken des alten table-lands häufte sich vulkanisches Material. Hausen spricht sich auch über abwärts gerichtete Vertikalbewegungen aus, indem er sagt, dass der Seeboden zwischen den Inseln sich bis zu 3000 m senkte.

Die entomologische Erforschung der Insel Tenerife ist eine Stütze für die Hypothese der Hebung und Senkung. Auf dieser Insel stehen in drei Teilen sehr alte Basalte an: Teno im N.W., Adeje im S.W. und Anaga im N.O. Das Zentrum der Insel ist von rezenten Eruptiven bedeckt. Die Fauna der drei erwähnten Gebiete bietet Elemente, die nur auf diesen Inselteilen vorkommen. Die Annahme ist deswegen berechtigt, dass es sich hier um drei frühere Inseln handelt, die durch die Entstehung des Vulkans Teide zusammengefügt worden sind.

Aus dem Vorkommen gemeinsamer oder vikariierender Arten auf zwei oder mehreren Inseln kann geschlossen werden, welche Inseln früher, welche später getrennt worden sind.

Geologische Erfolge (wie das Auffinden tertiärer Strausseneier durch Rothe—1964) bieten Datierungsmöglichkeiten für die Zoologen, welche es wiederum ermöglichen Aussagen über das Alter von endemischen und nichtendemischen Tieren zu machen, sowie deren Entwicklungsgeschwindigkeiten zu messen. Ansätze dazu sind bei den besser erforschten Tiergruppen bereits im Gange.

ZUR SPINNENFAUNA VON TENERIFFA

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Durch Untersuchungen von Lucas, Blackwall, Cambridge, Simon, Bösenberg, Strand, Dalmas, Caporiacco, Denis, Lampel, Cooke und eigene Arbeiten kannte man bisher 137 kanarische Spinnenarten, davon 78 von Teneriffa. Vom 8.–28.10.1961 konnten 60 Spezies in 9 Zonen gesammelt werden:

	Zone	*Zahl der Arten*
1.	Brandungszone der Nordküste	11
2.	Höhlen der Nordküste	7
3.	Küstenstädte	41
4.	Bananenplantagen	39
5.	Waldgebiete der Cordillera dorsal und des Anagagebirges	18
6.	Gebiet der Canadas	5
7.	Kiefernzone im Südosten	4
8.	Hochgebirge (Teide)	5
9.	Wüste im Südosten (El Medano)	4

Höhengliederung:

0–900 m über dem Meeresspiegel = Sukkulentenregion = unterhalb der Wolken: Zone 1–4 und 9;

900–1500 m über dem Meeresspiegel = Baumheiden-, Lorbeer- und Koniferenregion = im Gebiet der Passatwolken: Zone 5 und 7;

1500–3718 m über dem Meeresspiegel = Retama- und Pikregion = oberhalb der Passatwolken: Zone 6 und 8.

Zu 1: Felsen: *Steatoda grossa* und *Oecobius annulipes.* Erstere läßt sich überfluten und nährt sich dort von Kleinkrebsen. Grobes Geröll: *Hasarius adansonii**. Steinstrand: *Steatoda grossa, Steatoda nobilis,* dort wachsende Pflanzen: *Metargiope trifasciata, Dendryphantes moebii, Anelosimus aulicus.* Sandstrand: Irrläufer aus den Bananenplantagen.

Zu 2: Höhleneingänge: *Zygiella x-notata.* Höhleninneres in Nähe des Erdbodens: *Spermophora elevata**. Praktisch überall, am weitesten ins Innere vordringend: *Tegenaria parietina.* Gesteinsspalten: *Zoropsis rufipes.* Unter Steinen: *Drassodes riedeli***.

Zu 3: Außenwände der Häuser: *Filistata nigra***, ersetzt dort fehlende Amaurobiusarten; Beute wird nach Tötung eingesponnen; ein Weibchen lebt seit 1961 in Gefangenschaft; ferner *Segestria florentina, Steatoda nobilis, Zygiella x-notata, Dictyna guanchae***; die Weibchen unterscheiden sich von *D. civica* durch ganz flach gebogene Receptacula und eine an *D. sedilotti* erinnernde Zeichnung, Körperlänge 1,4–1,6 mm. Außenwände, Inneres dei Häuser, Hafenmauern: *Menemerus bivittatus**. Blüten: *Dictyna* (*Ergatis*) *walckenaeri vulnerata***.

Zu 4: Unterseite der Bananenblätter: *Theridion orotavense***, ein naher Verwandter von *Th. pallens,* häufigste Bananenspinne. Fruchtstände: *Steatoda nobilis,* häufigste Art Teneriffas, *St. grossa, Oecobius annulipes, Oe. immaculatus**, *Theridion musivivum**, *Araneus crucifer, Cyrthophora citricola, Philodromus punctigerus, Chalcoscirtus infimus***, *Hasarius adansonii, Jacobia brauni**, *Dendryphantes moebii, D. catus.* Bananenblüten: *Xysticus lucasi***, nahe verwandt mit *X. tortuosus.*

Zu 5: Gebüsch: *Zygiella x-notata minima***, 2,5 bzw. 3,2 mm große Zwergform mit gegenüber der hier fehlenden Stammart spitzerem Paracymbium. Unter Eukalyptusrinde: *Olios prominens,* wahrscheinlich identisch mit *Delena canariensis* Lucas, *Clubiona decora**, *Micaria gomerae**; von letzterer leben bis zu 30 reife Exemplare gesellig in einem Nest. Am Bäumen: *Dendryphantes catus**. Wegränder: *Agelena canariensis, Steatoda nobilis.*

Zu 6: Unter vulkanischem Gestein und Asche: *Haplodrassus dalmatensis, Steatoda grossa, Zelotes teidei***, eine Art mit unbewehrtem Metatarsus I, 5/2 Chelizerenzähnen, keulenförmigen und nicht rückwärts gebogenen sekundären Receptacula ähnlich *Z. oblongus.* Gartenpflanzen: *Araneus armidus***.

Zu 8: Beide Steatodaarten, *Haplodrassus dalmatensis**, *Zelotes teidei,* Salticide.

Zu 9: Unter Steinen: *Steatoda grossa, Cheiracanthium pelasgicum**. Unter Pflanzen: *Nomisia fortis**. An Pflanzen: *Araneus* sp.

Von diesen Arten leben in: Europa 31, Asien 14, Afiika (exkl. Mediterrangebiet) 19, Nordamerika 7, Südamerika 7, Australien u. Ozeanien 8.

Von den gesammelten Spezies bewohnen gleichzeitig: Mediterrangebiet 34 (ca. 60%), Atlantische Inseln 34, davon Madeira 31 (=53·4% der auf Teneriffa gesammelten).

Von den auf Teneriffa gefangenen Arten leben auf: Gran Canaria 22, Gomera 17, La Palma 6, Lancerote 5, Fuerteventura 2.

Biogeographische Verteilung der gesammelten Arten: Endemisch 20 (34·5%), Atlantisch 7 (12%), Mediterran 9 (15·5%), Paläarktisch 6 (10·2%), Paläotropisch 5 (8·6%), Zirkumtropisch 4 (7.0%), Kosmopolitisch 4 (7·0%), Transgredierend 3 (5,2%).

*Neu für Teneriffa **Neu für Kanaren

PATTERNS OF MIGRATION OF PLAGUE POPULATIONS OF THE RED LOCUST (*NOMADACRIS SEPTEMFASCIATA* SERVILLE)

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The red locust generates distinct plagues during which swarms can be found over much of Africa south of the Sahara Desert. The locusts involved in such plagues are thought to be derived from swarms escaping from the small number of regions where swarms can be formed from a non-swarming population; these are the "outbreak areas". The red locust breeds during the wet season and spends the dry season in adult diapause.

The most recent plague of the red locust lasted from 1930 to 1944. During the last twelve years of this period there was a recurrent pattern of swarm movement. Swarms migrated from southern Nyasaland, eastern Southern Rhodesia and the lower Zambezi valley, north and west into the Congo and Angola early in the dry season, and from the Congo south across western Southern Rhodesia and Bechuanaland into the Republic of South Africa, later in the year.

Breeding and probably swarm survival were much better in the wetter areas, which include the inception area of the annual migration, than the drier areas, which include the terminating points of the regular swarm displacements. Hence, it is suggested, the maintenance of the plague depended on the retention of at least part of the swarm population in the wetter areas.

A red locust plague generating model is proposed depending basically on three qualitative events, namely the generation and escape of swarms from an outbreak area, the transfer of these swarms or their progeny to southern Nyasaland, eastern Southern Rhodesia and the lower Zambezi valley, and the retention and final elimination of a swarm population in that area. This is a non-density dependent population model but since plague populations do die out there is no reason to search for density-dependent control.

Though red locust swaims most probably move down-wind it is not known why, of a swarm group, some remain effectively static while the rest move at various speeds. Further, since outbreak area populations are probably persistent, the survival advantage for the species of the mechanism of plague generation, as distinct from outbreak aiea swarm escape, is not obvious.

COMPOSITION ET ORIGINE DE L'ENTOMOFAUNA COMORIENNE

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L'archipel des Comores paraît tout entier d'origine volcanique récente, les basaltes les plus anciens étant néogènes et d'importants remaniements ayant eu lieu au pleistocène. La surface totale de l'archipel est de 1·884 km2 et les altitudes maxima varient selon les îles de 660 m à 2·351 m. L'ensemble est situé à mi-chemin entre le Nord de Madagascar et la Côte d'Afrique orientale, en zone tropicale humide.

La faune entomologique connue comprend 1·106 espèces, réparties en 767 genres, avec une dominance très nette des Coléoptères (427 espèces), Lépidoptères (287 espèces), suivis de loin par les Orthoptéroides (85 espèces) et les Hétéroptères (87 espèces). L'endémisme générique est très faible avec 1,3%, l'endémisme spécifique ou subspécifique par contre atteint 34%. L'indice de diversité spécifique se situe également à un niveau très bas: 1,44.

La comparaison de la faune des diverses îles est très difficile à faire car les chasses provenant des diverses îles ne sont pas comparables. Malgré ces réserves, la composition de la faune des quatre îles est sensiblement identique; l'élément endémique est quantitativement le plus important, suivi en quantités sensiblement égales par des éléments d'origine malgache et par des éléments d'origine africaine ayant, dans 50 à 70% des cas, atteint aussi Madagascar.

L'analyse des répartitions des vicariants subspécifiques, malheureusement relativement peu nombreux, fournit des enseignements précieux. Dix sous-espèces comoriennes sont des vicariants d'espèces africaines inconnues de Madagascar: de ces sous-espèces pas moins de 9 se trouvent à la Grande Comore et 5 ne se trouvent que dans cette île, la plus occidentale du groupe. Douze sous espèces comoriennes sont des vicariants d'espèces malgaches, de celles-ci 6 se retrouvent à la Grande Comoie et 5 ne se trouvent pas ailleurs. Trois sous-espèces sont des vicariants comoriens d'espèces afro-malgaches sans doute d'origine africaine et toutes trois se trouvent à la Grande Comore. Enfin une sous-espèce de la Grande Comore est un vicariant d'une espèce répandue dans la région orientale.

L'analyse de détail de la composition même de la faune comorienne fait ressortir l'absence des groupes les plus caractéristiques de la faune malgache: citons les Pogonostomes parmi les Carabiques, les Hexodon, les Cétonides, les Epilissiens, les Orphnides et les Ochodéides parmi les Scarabéides. Les formes d'origine malgache appartiennent en majorité aux groupes les moins spécialisés et par suite les moins anciens, dont les affinités africaines sont toujours plus nettes.

L'étude de la distribution des endémiques entre les diverses îles de l'archipel est très instructive. Il y a un nombre très important d'endémiques limités à une seule île: 100 à Mayotte, 88 à la Grande Comore, 75 à Mohéli et 29 à Anjouan. Mais le nombre d'espèces propres à deux, ou à trois îles est sensiblement du même ordre.

L'analyse de cette faune amène à considérer que les Comores ont reçu au moins l'essentiel de leur faune à une période très récente, sans doute contemporaine des remaniements pleistocènes.

Les éléments qui ont colonisé les Comores viennent, en partie égale, des deus masses importantes voisines: Afrique et Madagascar. De ce fait la faune comorienne est un mélange, en constant remaniement, de faunes distinctes.

A ces éléments introduits par voie naturelle, s'ajoutent bien entendu des éléments plus récentes encore, apportés par l'homme et particulièrement nombieux à Mayotte et à Mohéli où la colonisation humaine a été plus active qu'à la Grande Comore. Enfin de nombreuses espèces sont subcosmopolites et ont pu être introduites n'importe quand au cours des deux derniers millénaires.

Tout nous porte donc à considérer que les Comores sont un archipel à peuplement récent, dont la faune (comme la flore) montre un très faible dynamisme, une faible tendance à la spéciation, et une distribution due aux faits de hasard et non à l'existence de liaisons terrestres soit entre îles de l'archipel, soit entre l'archipel et les terres voisines.

LA FAUNE NOTODONTIENNE MALGACHE COMPAREE AUX FAUNES SIMILAIRES ETHIOPIENNE ET ORIENTALE

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La faune Notodontienne Malgache compte 65 espèces réparties dans 26 genres, dont 7 ou 8 sont connus également du continent Africain et, pour deux d'entre'eux, des régions Paléarctique et/ou Orientale.

Toutes les espèces Malgaches sont endémiques. Peu d'espèces appartiennent aux genres pan-Africains ou paléogées:

Rhenea	1 espèce Malgache sur	4
Scrancia	2	40 env.
Antheua	1	28
Phalera	2	7
Elaphrodes	1	4
Tricholoba	1	8
Desmeocraera	7	80 env.
Atrasana	2	12

Ces 17 espèces sont probablement les endémiques les plus récents.

Plusieurs genres sont les vicariants Malgaches de genres Ethiopiens:

Analama, Ambina	/ *Scalmicauda* et voisins
Griphocerura, Antongila,	
Chlorocalliope, Vietteella	/ groupes "aberrants" du complexe *Desmeocraera*
Eutrotonotus	/ *Clostera*
Nesoptilura	/ *Ptilura*
Pachycispia	/ *Trotonotus*
Acrasiodes	/ complexe "*Chadisra*"

Ces endémiques ont une origine plus ancienne, avec différenciation ayant atteint le niveau générique.

Les genres *Malgadonta*, *Romaleostaura*, *Antsalova*, *Italaviana* correspondent au complexe *Eurystaura* du continent, mais sans affinités nettement définies. Les genres *Schedostauropus* et *Spodiosomera* n'ont pas d'équivalant Ethiopien. Leur position est analogue à celle des genres "aberrants" du complexe *Desmeocraera* et leurs vicariants Malgaches (*Griphocerura* etc.) qui n'ont en réalité que le faciès de commun avec *Desmeocraera*. Les endémiques de cette catégorie sont sans doute les plus anciens.

En résumé, 100% des espèces et 70% des genres Malgaches sont endémiques. Des 30% des genres restants, 22% sont pan-Africains et 8% seulement paléogées.

Les affinités des genres endémiques se trouvent être nettement en direction du continent Africain. On peut dire que l'admixtion directe d'éléments Orientaux est nulle. Les affinités Orientales ne sont que secondaires, dans le cadre plus large de la faune Notodontienne pan-Africaine. Il s'agit de grands complexes comme ceux de *Desmeocraera*, de *Scrancia*, de *Chadisra* et autres, avec une large vicariance Africaine—Orientale et/ou Paléarctique. Une mention spéciale revient au genre semi-cosmopolite *Clostera* qui ne montre pas de différenciation géographique, sauf précisément à Madagascar (genre vicariant *Eutrotonotus*).

La composition et l'origine probable de la faune Notodontienne Malgache sont donc très nettement Africaines, ce qui fournit un argument de plus contre l'existence de la Gondwanie classique, c'est à dire comprenant la Lémurie comme un pion essentiel. Même en admettant l'existence dans le passé d'une Gondwanie amendée, sans la Lémurie (nous ne discuterons pas ici du nom à donner à un tel complexe), on reconnaîtra la probabilité d'une origine du peuplement Notodontien de la Grande Ile postérieure à la désintégration de cette "Gondwanie". L'élément à considérer en premier lieu est la jeunesse géologique relative des Notodontidae (Oligocène?). L'époque de la séparation de Madagascar du continent Africain n'a ici qu'une importance toute relative, étant donné l'exiguïté de la "barrière" et tenant compte des théories récentes sur les moyens de dispersion des organismes.

ETUDE DES RELATIONS GEOGRAPHIQUES DES LAELAPS DE L'AFRIQUE SUBSAHARIENNE

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Il y a actuellement 34 espèces de *Laelaps* connus en Afrique Subsaharienne, y compris *Echidnolaelaps.*

La répartition géographique de ces espèces montre que la Sous-Région Occidentale héberge 17 espèces dont 13 endémiques. La moitié de ces espèces présentent une spécificité d'hôtes soit absolue soit quasi-absolue, et la plupart des autres espèces sont inféodées à des rongeurs de répartition discontinue en raison de leurs biotopes particuliers ou de leur moeuis. La dispersion des *Laelaps* parasites s'en trouve donc fort limitée. Parmi ces espèces sous-occidentales, deux, *L. echidninus* et *L. praomyia* montrent une nette tendance à la dispersion au delà de la Sous-Région.

La Sous-Région Orientale ne comporte que deux endémiques.

Cinq espèces ont une répartition occidento-orientale mais sont souvent marginales pour la Sous-Région Occidentale.

Les espèces Sud-Africaines endémiques sont au nombre de 6.

Il y a de plus 7 espèces holosubsaharienne dont *L. nuttalli* qui semble mal adapté aux Muridae africains. L'éventail des hôtes de ces espèces holosubsahariennes est très large en général: 10 à 20 genres de rongeurs.

Discussion: La zone Ouest du bloc forestier congolais paraît particulièrement représentative de la faune laelaptidienne de la Sous-Région Occidentale. Elle est assez bien isolée géographiquement par deux frontières écologiques, le Congo au Sud et une zone de forêt marécageuse au Nord de sorte que les apports extéiieurs y sont faibles et ne portent que sur 6 espèces sur 17. Parallèlement l'endémicité des espèces y est grande puisqu'elle est de 11 espèces sur 17 soit 64%. Dès qu'on s'écarte de cette région centrée sur Brazzaville, le nombre des endémiques diminue sensiblement et les apports extérieurs augmentent. C'est le cas de la région de Bangui au Nord et de Dundo (Angola) au Sud qui sont situés au-delà des deux barrières écologiques mentionnées plus haut, et où le nombre des endémiques tombe à 30%. C'est le cas également de la partie Ouest de cette Sous-Région (Côte-d'Ivoire) où un seul endémique a été trouvé.

La Sous-Région Sud-Africaine est aussi un foyer bien individualisé pour la faune laelaptidienne. Elle possède 46% d'endémiques.

La Sous-Région Orientale en dehors de ses deux espèces endémiques a une faune d'apport Occidental en premier lieu, Sud-Africain pour une plus faible part, le reste étant constitué d'espèces holosubsahariennes.

Il semble donc que l'on puisse parler en Afrique de deux foyers principaux de *Laelaps:* l'un congolais, le plus important dont les axes de dispersion sont orientés en direction de l'Uganda et vers le S.E. vers le Katanga, l'autre, Sud-Africain essaimant vers le Nord et la Sous-Région Orientale.

L'apport paléarctique est très faible: deux espèces seulement.

A propos des conditions même de dispersion il semble que ce soit la faculté d'adaptation à un ou plusieurs hôtes qui commande en fait la dispersion, les espèces largement répandues étant celle qui sont adaptées aux rongeurs à distribution continue: *Lemniscomys, Mastomys, Praomys.* Cependant certaines exceptions à ce schéma montrent que des facteurs écologiques propres à l'espèce et indépendants des hôtes entrent aussi en jeu: par exemple *L. nuttalli* à qui son adaptation aux *Rattus rattus* n'a pas suffi pour une dispersion totale.

SECTION 8.—INSECTICIDES AND TOXICOLOGY

The following papers were read but their authors did not wish them to be published here:

Gasser, R., Grob, H., Ruzette, M. A. and Wyniger, R. (Switzerland). Die Probleme bei der Bekämpfung von Vorblutenschädlingen im Obstbau.

Pradhan, S. (India). A new physical theory of the mode of action of DDT.

Williams, C. M. (U.S.A.). Hormones interfering with insect development.

CONTRIBUTED PAPERS

HEUTIGER STAND DES GETREIDELAUFKÄFER-PROBLEMS IN JUGOSLAWIEN UND METHODEN ZU SEINER LÖSUNG

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Der Getreidelaufkäfer ist im Jugoslawischen Weizengebiet überall allgemein, doch das Zentrum des Verbreitungsareals befindet sich im südlichen Teile der Pannonischen Ebene (Provinz Voivodina).

Mit der Einführung in die Praxis der italienischen Weizensorten (1957) wurde der Getreidelaufkäfer-Befall sehr begünstigt, denn wegen der möglichst frühen Saat dieser Sorten wird man oft gezwungen den Weizen wiederholt auf denselben Flächen zu bestellen. Ausserdem, der grosse Kornausfall dieser Sorten und die Combine-Ernte haben anstatt eines Herdenbefalls, dort wo die Garben standen, einen difusen Befall über die ganze Oberfläche, als Folge.

Das Getreidelaufkäfer-Problem bedürft in Jugoslawien noch weiterer Klärung dreier Fragen: des Vorkommens anderer Laufkäfer-Arten derselben Gattung und ihrer Beziehungen zum Getreide, der Sommerdiapause und der praktischeren und leichter durchführbaren Bekämfungsmethoden.

Was die Bekämpfung betrifft, wurden von den Verfassern zwei, bzw. drei Verfahren entwickelt, bei denen die Bekämpfung vorgeschoben und gegen die Imagines gerichtet wird. Das Erste ist eine Fang-Kanäle-Methode die mit der Anwendung von nur 12-15 kg/ha des Insektizides gute Resultate sichert. Mit dem Traktor wird es, auf einer Entfernung von zirka 25 m. kreuz und quer über die Parzelle gefahren, die mit Getreide bestellt war und wieder bestellt werden soll. Immer nur eine Traktor-Spur wird gleichzeitig mit Lindane, Aldrin oder Heptachlor bestäubt, zirka 1,5 kg/100m Länge. So bekommt man einen Netz über der ganzen Acker-Oberfläche und die Käfer müssen in ihrem Herumlaufen darübertreten.

Bei der zweiten Variante dieses Verfahrens wird die Bestäubung der ganzen Oberfläche mit der Kunstdüngung kombiniert und um die schon erwähnte Zeit durchgeführt. Hier werden 20 kg/ha Aldrin + 450 kg/ha NPK-Dünger vewandt, und zwar nach dem Pflügen, dass erst nach zirka 10 Tage wiederholt werden soll.

Das zweite Verfahren, auch gegen die Imagines gerichtet, ist ein Lock-Verfahren. Hier wird die Eigenschaft der Käfer ausgenützt, sich unter den Stroh-Ballen zu versammeln. Mindestens 25 Stroh-Ballen pro ha sollen auf dem Acker verteilt werden, nachdem die Bodenfläche, die von den Ballen bedeckt wird, mit Lindane, Aldrin oder Heptachlor in einer Menge von 10 dk/m^2 bestäubt wird.

Wenn die Bekämpfung der Käfer aus irgend welchem Grund nicht durchgeführt werden kann, dann werden die Larven bekämpft, aber nicht nach dem Erscheinen der ersten Schäden, wie früher üblich, sondern gleichzeitig mit der Saat und mit den Kunstdünger kombiniert. Die Insektizid-Kunstdung-Mischung wird in die Tiefe von 2-3 cm unter dem Saatgut eingebracht um die eventuelle phytotoxische Wirkung auf die Keimlinge zu vermeiden.

Es ist zu empfehlen während der Sommerdiapause der Käfer, d.h. im Juli-Anfang August, Boden-Proben von 50 × 50 × 40 cm zu entnehmen um entscheiden zu können welche Parzellen können ohne dem Einsatz chemischer Bekämpfungsmasnahmen mit dem Getreide wiederholt bestellt werden. Dabei wird eine Populationsdichte von 700 Käfer pro ha als niedrig, von 700-2500/ha als mittel und über 2500/ha als hoch geschätzt. In den Fällen wo die wiederholte Getreidesaat auch an den mittel, oder sogar an den stark besiedelten Parzellen stattfinden muss, muss dan die chemische Bekämpfung nach einem der erwähnten Verfahren durchgeführt werden, während sie bei der Besiedlung Zero, oder bei einer nur schwachen Populationsdichte ausgelassen werden kann.

THE ROLE OF OXYGEN IN THE TOXICITY OF FUMIGANTS TO INSECTS

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Although oxygen is essential in the normal metabolism of insects it can be toxic when applied to insects that have been treated with sublethal doses of certain insecticides. Oxygen can potentiate the action of at least seven different poisons to two species of insects. With respiratory poisons such as hydrogen cyanide the effect of oxygen presents a certain paradox; oxygen helps to reverse the inhibition so that respiration is resumed, but more insects die than when oxygen is excluded and respiration delayed (2).

To investigate further the potentiating action of oxygen on poisoned insects certain aspects of the metabolism of *Sitophilus granarius* L., poisoned with hydrogen cyanide and subjected to various oxygen tensions were studied. The levels of glycogen, α-glycerophosphate, lactate, pyruvate and citrate in normal and poisoned insects were determined to investigate the role of oxygen in the utilization of these metabolites. Investigation was made both on unpoisoned insects and on insects treated with cyanide and then placed in atmospheres of 0, 21 and 100% oxygen for 48 hours. The results were compared with the mortality occurring in the insects subjected to the various treatments.

Alteration of the oxygen tension of the atmosphere from normal to abnormal tensions exerted a stress on the insects which caused increased utilization of glycogen and the accumulation or, in some cases, the depletion of other metabolites. When insects were placed in nitrogen (0% oxygen) the level of α-glycerophosphate increased only slightly, pyruvate accumulated to twice its normal level and lactate accumulated to 46 times the normal level. When treated with cyanide and retained in nitrogen there was no abnormal accumulation of pyruvate but lactate accumulated as it did when unpoisoned insects were retained in nitrogen. More glycogen was utilized by insects in nitrogen than by cyanide-poisoned insects in nitrogen. When poisoned insects were placed in 100% oxygen respiration was resumed, the lactate level decreased but pyruvate increased to five times the normal level, citrate to nearly three times normal and the mortality was 99%.

From the results obtained it is quite evident that oxygen tension has profound effects on the metabolism of *S. granarius*. The potentiating effect of oxygen may well be associated with interruption of one part of the metabolic system even while there is reactivation of another. The accumulation of pyruvate in the presence of oxygen indicates that oxygen prevented pyruvate from being converted to lactate or from being further metabolized even while respiration, which was initially inhibited, was being reactivated. Furthermore, the results indicate that the toxicity of cyanide to *S. granarius* is a complex situation that is intimately associated with oxygen tension. Indications are that cyanide-poisoning does not closely resemble effects brought about by physical exclusion of oxygen alone. The possibility that the toxicity of cyanide to these insects is simply due to inhibition of cytochrome oxidase alone is unlikely. This conclusion agrees with previous results which showed that the response of *S. granarius* to anoxia differed markedly from its reaction to cyanide (1, 2).

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STUDIES ON THE OVICIDAL ACTION OF PETROLEUM OILS

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In seeking to overcome the obvious disadvantages of the synthetic organic insecticides, we have undertaken a re-evaluation of petroleum oils. Among the advantages of this class of insecticides are: (1) they leave no toxic residues (2) insect resistance to them has not occurred despite over a half century of use against a wide variety of pest species. Little is known of the mode of their ovicidal action and this poses a bottleneck in our quest for the ideal hydrocarbon molecule which might be derived from sources other than petroleum oil.

It was not until 1947 that the effect of petroleum oil on the respiratory rate of developing eggs was determined. These studies (3) established three significant points:

(1) oil treatment depressed respiration;
(2) depression for about 24 hours resulted in death of the embryo;
(3) oil induced its lethal effect by physical means without penetrating the chorion.

These time-mortality relations could be readily explored by removing the oil from the surface of the chorion at intervals after treatment by rinsing the eggs in harmless solvents such as petroleum ether.

These results suggested that volatility was the key to ovicidal efficiency. Investigations on the relationship of chemical composition to ovicidal efficiency have been continued (2) within a framework dictated by natural conditions and the work cited earlier. Thus, volatility was determined under the following test conditions:

(1) Temperature, that occurring in actual usage (80°F).
(2) Time, a 24-hour period.
(3) Oil deposit, a thin film on a non-porous surface.

These conditions were met by spraying oil on sheets of aluminium foil and plotting rate of volatility based on weight loss over the 24-hour period. Based on volatility curves the oils fell into three general categories: (1) ineffective oils, those volatilizing within 12 hours, (2) moderately effective oils, those volatilizing in over 12 hours, (3) highly effective oils, those with little or no volatilization in 24 hours. In terms of molecular weight, maximum ovicidal efficiency was reached at a molecular weight of approximately 320 regardless of oil type, volatility being minimal at this point. This simple test did much to explain the relationship of the standard physical measurements, i.e. boiling point and molecular weight to ovicidal efficiency (1).

More recently we have considered the susceptibility of eggs whose respiration occurs through pseudomicropiles to determine the relationship of this adaptation to susceptibility. The egg of the large milkweed bug *Oncopeltus fasciatus* (Dall.) was used. The results established the following points:

(1) Only the pseudomicropiles need be covered to effect kill.
(2) Oil could not be washed from the egg following treatment as could be done with the oriental fruit moth egg.
(3) The response of the milkweed bug egg to treatment with naphthenic, paraffinic, and isoparaffinic oils revealed the same relationship between type and efficiency as in the case of the usual oil susceptible species such as the oriental fruit moth which do not possess pseudomicropiles.

Tests have been underway to determine the range in susceptibility of insect eggs. An atypical example has been found in the egg of the pear psylla *Psylla pyricola* Foerst., which is not killed at levels as high as 40% oil and oils ranging in viscosity from 30 to 500 seconds (SUS at 100°F) appear to be equally ineffective.

These results are of particular interest as they relate to mode of action and development of resistance. It would seem unwise to conclude that susceptible species cannot acquire resistance when related species have natural resistance.

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THE INFLUENCE OF INSECTICIDES ON SOIL LIFE

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The use of chemical pest-killers in some cases stimulates the microflora and invertebrate animal activities and gives rise to increased yield of agricultural crops (Bogdarina 1952; Bershova, 1952; Bezzub, 1952; Grigoryeva, 1952; Arkhangelskaya, 1955; Ivanova, 1958, etc.).

There are however, opposite opinions (Shieals, 1951; Ripper 1959; Klokke 1953; Bovey 1955, etc.), that the carrying of insecticides into soil disturbs the biological balance of all soil animal groups. We do not deny the possible positive effect of insecticides on the yield of crops but it takes place because the soil becomes rich in biomass both of invertebrates and bacteria. This biomass contains all the necessary elements for plant nutrition. But there are no methods for the absolute calculation of living soil organisms.

For this reason we studied the influence of BHC and heptachlor on living soil organisms, by the mobility of organic substances and also measuring the carbon dioxide of the soil. These results permit us to calculate the number of organisms dying from insecticides.

The experiment took place on chernozem soils treated with 50 kg per hectare of 25% dust BHC for sugar beet and in laboratory conditions on the same soil with calculation of the carbon dioxide.

Analysis of soils in the field experiments were carried out three times during the vegetative season and in the laboratory only once—at the end of tests (after 2·5 months).

The results of the experiments testify to considerably stronger action of BHC on the living part of soil. Increase in the biomass took place only at the first date of taking samples, i.e. soon after applying BHC to the soil. At the next dates of taking samples (22·8–21·10) one could not find any considerable influence of BHC on the increased amount of the insoluble organic substances in soil. We concluded that the high increase of the insoluble organic substances in the soil found at the first date on the BHC plots is caused by annihilation of soil invertebrates and probably some groups of microorganisms, the biomass of which has been used by plants at the next time of taking samples.

The action of BHC and heptachlor in the laboratory was quite peculiar. They do not diminish the nitrification, but highly increase the ammonification. The accumulation of ammonium increased more than three times in comparison with the control. This experiment seems to explain increased accumulation of ammonium on soil after its sterilisation and drying out (Rassel 1955).

By the amount of carbon dioxide from soil we noted the considerable difference in the action between BHC and heptachlor. Carbon dioxide was given off from soil actively in the experiment with heptachlor.

By chemical control or in other cases when pest-killers get into soil, their influence on the life processes in the soil must be taken into consideration. Determination of content of soluble organic substance and nitrogen combinations in soil after use of organic insecticides will be a more reliable method for calculation of their influence.

HORMONAL IMBALANCE IN MICE FED CONTINUOUS LOW LEVELS OF CHLORINATED ORGANIC INSECTICIDES

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This paper reports some of the effects on reproduction in the BALB/c strain laboratory mouse, and their progeny, of continuous, sublethal, dietary levels of three organochlorine insecticides, Kepone, Mirex and Telodrin.

Theoretically, four affects could be observed: (1) No affect, either in litter size or frequency; (2) decreased reproduction by decrease in litter frequency, with normal litter size; (3)

decreased reproduction by decrease in litter size, with normal frequency; and (4) increased reproduction by increased litter size, frequency or both.

Kepone indicated a decreased reproduction by decrease in litter frequency with normal litter size. Mirex appeared to decrease reproduction by decreasing litter size, with normal litter frequency. Telodrin seemed to increase litter frequency, with no affect on litter size; however, survival of young was quite low.

In detailed studies of the Kepone influence, the number of young produced by Kepone-fed females was reduced by 24%, 79% and 87% at dietary levels of 10, 30 and 37·5 ppm, respectively. Females fed 40 ppm 60 days before and during reproductive tests failed to produce any litters. Matings between test females and control males produced no litters, while control females did produce litters by test males. Reproduction resumed within seven weeks in treated females following the withdrawal of Kepone.

Vaginal smear data indicated a definite disturbance of the estrous cycle in test females, 85-90% being in constant estrus. Histological examination of their ovaries revealed normal follicle development, but usually no corporea lutea. Gonadotrophin bioassays, using the ovaries and ventral prostates of rats as indicator organs of follicle stimulating hormone (FSH) and luteinizing hormone (LH) activity, respectively, revealed that the pituitaries of test females equalled the controls in FSH activity, but a loss of 25% LH activity. This reduction in LH activity may be sufficient to prevent ovulation, mating, and consequently reproduction. This disturbance may lead to prolonged FSH stimulation and constant estrogen secretion from the large follicles producing the sterile, constant estrus condition.

With this position it appeared necessary to measure the estrogens in the urine of test mice, both qualitatively and quantitatively. Extraction of the estrogens and conversion to the esters of acetic anhydride followed by argon ionization gas chromatography did not prove sensitive enough for our purposes, as did the chloro-acetic anhydride esters which were gas chromatographed using electron capture detection. Preliminary work with microfluorometry has shown that as little as 0·5 nanogram of estrone and estradiol and 5·0 nanograms of estriol can be determined with accuracy.

A STUDY ON THE HERITABILITY OF THANATOSIS AND THE INSECTICIDE TOLERANCE OF SELECTED POPULATIONS OF *CALANDRA GRANARIA* L.

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Thanatosis or death feigning is a nervous response and is well developed in many insects, which assume an immobile posture by tightly pressing legs and antennae to the body. Preliminary experiments suggested an uneven distribution of periods of thanatosis within a population of a species. Besides the normal duration of thanatosis of *C. granaria* which ranges from 4 to 6 seconds, a few very high (18 seconds) and low (0 second) values have been recorded. The persistence of insects showing higher and lower periods within all cultures from generation to generation led to the undertaking of a selection experiment, in order to throw light on its cause.

Further, it was considered interesting to determine whether any differential susceptibility to insecticides exists among these different strains of beetles which occur within a population; those highly sensitive, showing a duration of thanatosis of more than 8 seconds, and those less sensitive, showing a duration of thanatosis ranging from 0 to 3 seconds, to the stimulus.

Selection experiments were performed. Insects showing longer periods of thanatosis, from one population and insects showing shorter periods of thanatosis, from another population, were eliminated by selection, thus providing two lines. A duration of 8 or more seconds was chosen as the longer period of thanatosis and 3 or less seconds as the shorter period. Insects showing duration of thanatosis in between these values were rejected. Five or more selections were carried out in each generation. As a result of selection in successive generations

the percentages of the insects having the longer periods of thanatosis and of those having the shorter periods of thanatosis were increased in the 6th generation to 96 and 94 from 17 and 31 respectively. The percentage increase in the number of insects showing longer or shorter periods of thanatosis as a result of repeated selections in each generation was almost identical after 1st generation. These figures indicate the probability of thanatosis being a heritable character.

Further, a few experiments were performed to investigate the relation between the susceptibility to insecticides, judged by paralysis, and the susceptibility to a mechanical stimulus judged by the duration of thanatosis, in two strains of the weevils studied. The strains were selected on the basis of their behaviour to mechanical stimuli, the duration of thanatosis in one strain being much longer than in the other. Both the selected strains were assayed against DDT, pyrethrum and nicotine. The two sets of concentration-response lines are not coincident and the Median Response Concentrations are considerably different for the two strains:—

MEDIAN RESPONSE CONCENTRATIONS

Calandra granaria	*Median response concentrations*		
	Pyrethrum	*DDT*	*Nicotine*
Weevils showing longer periods of thanatosis	0·275%	0·628%	0·035%
Weevils showing shorter periods of thanatosis	0·492%	0·827%	0·057%
Control	0·379%	0·76%	0·04%

Since insects which are very sensitive to mechanical stimuli are also very susceptible to insecticides, it is possible that some cells in the cuticle which are very sensitive to mechanical stimuli are also very sensitive to these insecticides. Without attempting to define an underlying mechanism common to the two responses the existence of a definite association between the two may be pointed out.

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THE SYNTHESIS AND BIOLOGICAL PROPERTIES OF NEW O-ALKYL-S-ARYL ALKYLPHOSPHONODITHIOATES

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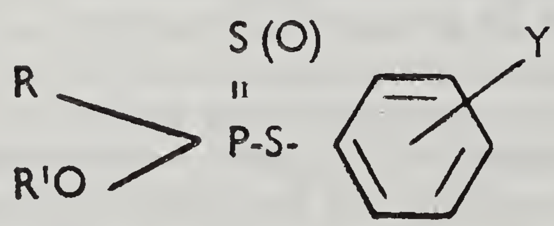
Although phosphate ester insecticides are widely accepted today and many papers have been published concerned with their chemistry, biochemistry and biological action, relatively few studies have been published dealing with a related group of insecticides: alkylphosphonate esters. Fukuto (2) reviewed the state of knowledge in this field and in collaboration with Metcalf and other co-workers (1) has systematically studied a large number of alkylphosphonic and thiophosphonic acid esters.

In the present investigation, the authors report on the synthesis, biological properties and structure activity relationship of a novel group of alkylphosphonodithioate esters. This series is represented by the following generalized structure:



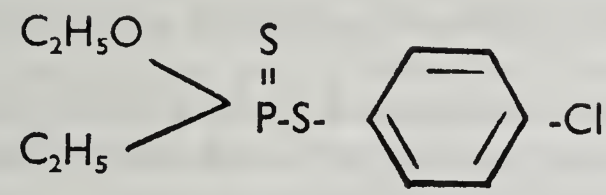
$R, R^1 = CH_3$ to C_3H_7

$Y = H, CH_3$ to C_4H_9, CH_3O, Cl

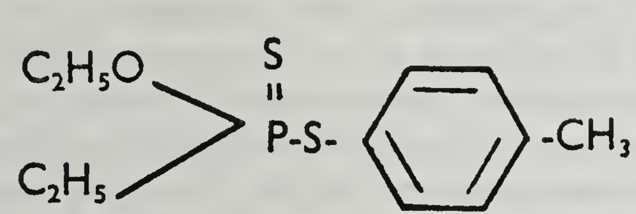
The method of preparing these compounds has been described by Szabo et al. (6).

The insecticidal properties of the subject compounds were evaluated against the house fly, *Musca domestica* L., susceptible, OP-resistant and multi-resistant strains; the spotted milkweed bug, *Oncopeltus fasciatus* Dallas; the American cockroach, *Periplaneta americana* L; and the salt-marsh caterpillar, *Estigmene acrea* Drury. Mammalian toxicity was established with male albino rats. Cholinesterase inhibition on paper chromatograms was determined along the lines described by Getz and Friedman (3).

Ring substitution whether electropositive or electronegative did not affect insecticidal activity significantly. The most toxic compound to insects and rats was one with a *p*-Cl substituent.



The preferred compound in this series, based on its selective insect toxicity was a member with a *p*-tolyl substituent.



High activity also was displayed by a series of unsubstituted O-Alkyl-S-Arylalkylphosphonodithioates. Highest overall activity was shown by (O-ethyl-S-phenylethylphosphonodithioate). A comparison between the phosphonate esters and two analogous phosphate esters showed decidedly the former compounds as the superior insecticides and most toxic to mammals. Varying the alkyl group R did not alter insecticidal activity significantly.

A comparison of two analogous pairs of phosphonodithioates with their corresponding phosphonothiolates showed that the latter possess similar toxicity against house flies but were significantly more toxic against rats and more inhibitory towards human plasma cholinesterase on paper chromatograms.

It was also observed that the phosphonodithioate (O-ethyl-S-phenylethylphosphonodithioate) was rapidly converted to its thiol analog during chromatography. It is speculated that this rapid conversion could account for its high toxicity. Possibly, intoxication largely predominated over detoxication, the latter not being able to exert its action due to the lack of an "opportunity factor" (5). Of considerable interest also was the comparative toxicity of certain phosphonodithioate and their phosphorodithioate analogs to susceptible and resistant house flies (parathion resistant and multi-resistant strains). These studies showed only "vigor tolerance" (4) toward the phosphonates and true resistance against the phosphate esters. Fukuto et al. (1) made similar observations in studying the comparative toxicity of a phosphonate analog of parathion to susceptible and resistant strains of house flies.

In conclusion, it appears that the C-P bond contributes greatly to the unique biological characteristics of these compounds. Altering Y substitution on the ring and the chain length of R and/or R'O resulted in a relatively minor change in insecticidal activity. These structural changes, however, did have a marked effect on mammalian toxicity.

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METABOLISM OF PHTHALIMIDOMETHYL-O, O-DIMETHYLPHOSPHORO-DITHIOATE (IMIDAN) IN WATER, INSECTS AND THE RAT

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In a previous paper the metabolism of the experimental insecticide Imidan (phthalimido-methyl-O, O- dimethylphosphorodithioate) in the cotton plant was reported (5). It was shown that C^{14}-Imidan was metabolized to phthalic acid (PA) and benzoic acid oı derivative(s) of the latter based on decarboxylation data, and radioscans of paper chromatograms.

In this study the fate of C^{14}-Imidan is described in aqueous media, the German cockroach and a male albino rat.

At pH 8·5 and room temperature the end products of hydrolysis, as determined by paper chromatography scans of radio-chromatograms and infrared scans, were phthalamic acid (PAA) salt and *O*, *O*-dimethylphosphorodithioic acid salt. At pH 4·5 PAA is gradually converted to PA.

Radioscans of chromatograms of internal acetone cockroach extracts indicated the presence of Imidoxon (phthalimidomethyl-*O*, *O*-dimethylphosphorothiolate) 2 hours after topical application of C^{14}-Imidan. Confirmation of the presence of Imidoxon was also obtained by co-chromatography using DCQ (5) and a cholinesterase inhibition detection method (2). Formation of Imidoxon also coincided with a rapid increase in intoxicated and moribund cockroaches. After longer holding intervals there appeared a polar metabolite which corresponded in Rf to PAA in an ethanol:water:NH_4OH (80:15:5) system.

In the course of the radioanalyses it became evident that there was an incieasing build up of non-acetone extractable radioactivity accumulating in tissues with time. The nature of the fixed activity was elucidated as follows:

Pooled acetone extracted tissue debris was hydrolyzed in HCl in the usual manner. The hydrolyzed residue was extracted with absolute ethanol and pyridine (4). Chromatography in a butanol:acetic acid:water (4:1:1) system yielded a radioactive peak corresponding to PA. The latter was also confirmed by co-chromatography with authentic PA. From this finding it appears that the bound activity existed in tissues in the form of a PA or PAA derivative, since both acids are freely soluble in acetone. The derivative could be bound to natural body constituents through hydrogen bonding.

Following the ethanol-pyridine solvent extractions there remained a significant amount of radioactivity (twice the specific activity found in the pre-hydrolyzed tissues) associated with the humin fraction (3). This suggests that a portion of the C^{14}-activity arising from Imidan was incorporated into carbohydrates and/or tryptophan and tyrosine. No detectable amount of $C^{14}O_2$ was collected from the cockroach cages.

Orally administered C^{14}-Imidan was rapidly eliminated in the urine and faeces of a rat. Ninety-eight percent of the radioactivity in urine (6 hours interval) was water soluble. Radioscans of chromatograms of the extracted urine yielded a major peak with the characteristics of of a conjugate. A hydrolyzed aliquot of the extracted urine yielded a single radioactive peak corresponding to PA. No $C^{14}O_2$ was collected indicating the absence of decarboxylation of the phthaloyl moiety. Faigle and co-workers (1) also failed to recover $C^{14}O_2$ from a C^{14}-phthalimido moiety when fed to rats and dogs.

In summary it appears that in the cockroach and rat the end products of C^{14}-Imidan metabolism consist of PA or PAA and derivatives, while in plants they are PA and benzoic or its derivative(s). PAA (alkaline pH) and PA (acid pH) are the aqueous hydrolysis end products. The nature of the derivatives is presently under further investigation.

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MECHANISM OF ACTION OF DDT IN *MUSCA DOMESTICA NEBULO* FABRICIUS —ROLE OF EPICUTICULAR WAX IN THE MECHANISM OF ENTRY

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The toxicity of p,p′-DDT as a contact insecticide in insects is guided by two factors, viz., its ability to penetrate the insect cuticle so as to gain access to the site of action followed by its toxicity at low concentration in the insect metabolism. There is, however, a considerable amount of speculation as to the exact mechanism involved in either of these processes (5). According to Richards and Cutkomp (3) chitinous cuticle facilitates the entry of DDT into the insect body by selective concentration through absorption. DDT may penetrate into the insect body by being dissolved in the epicuticular wax (1, 2, 4).

Studies on the role of epicuticular wax of house flies, *Musca domestica nebulo* Fabricius, in the mechanism of entry of p,p′-DDT in the body have been undertaken. Pure epicuticular wax of 4-5 days old adult flies was obtained by washing them with chloroform followed by treatment with pure acetone. Micro amounts of p,p′-DDT is added to the yellowish coloured wax. The melting point of the pure wax alone and in combination with varying amounts of DDT has been determined. For the sake of comparison melting point of bees-wax alone and in combination with p,p′-DDT was also determined.

The effect of DDT on the lowering of the melting point of the epicuticular wax is a very significant fact. The maximum lowering of temperature of wax takes place when the percentage of DDT is 15% i.e., from 29·5°C to 27°C. Any amount of DDT added beyond this level tends to raise the melting point of the epicuticular wax; while in the case of bees-wax the lowering of melting point goes on even up to 30% DDT i.e., from 68°C to 58·5°C.

It appears that with the lowering of the melting point of the epicuticular wax DDT gets a faster entry into the cuticle being in a semi-solid condition, which is brought about by gradual solution of DDT into the wax, where it is soluble. Further the micro-amounts of wax being in a semi-solid condition may also be penetrating along with DDT into the body fluids of the insect thus contributing to the toxicity of the insecticides. A similar phenomenon has already been observed in roaches with p,p′-DDT (4).

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MECHANISM OF ACTION OF DDT IN *MUSCA DOMESTICA NEBULO* FABRICIUS —INHIBITION OF THE ACETYLCHOLINESTERASE ACTIVITY

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The presence and kinetics of acetylcholinesterase activity in *Musca domestica nebulo* Fab., has been described and worked out in detail (4). An increase in the amount of the acetylcholine content in insects has been reported (5, 1, 3) and contradicted (2). There has been a great controversy as to the specific action of DDT on the cholinesterase enzyme.

The details of technique employed for the determination of acetylcholinesterase activity has been described in detail (4). In all the experiments 3 c.c. of buffer at 7 pH, 0·6 c.c. of substrate (acetylcholine bromide at 0·11 M) and 3 c.c. of brei (10 heads of abdomen or thorax or whole flies or thoracic ganglia) have been used and incubated at 37°C for one hour. The house flies (4-5 days old) have been treated with 1% solution of p,p′-DDT in acetone.

The cholinesterase enzyme has been determined in the treated and untreated flies at intervals of 1, 2, 4, 6 and 24 hours after insecticidal treatment. The inhibition of the enzyme

is 15·4%, 35·3%, 53·4%, 71·4% and 89·8% after 1, 2, 4, 6 and 24 hours. Enzyme activity was also determined in the head, thorax and abdomen of the treated flies after 1 and 2 hours. The inhibition of the enzyme is 9·3% and 15·5% in the heads and 11·5% and 22·7% in the thorax after one and two hours of insecticidal application respectively. In the case of the abdomen the enzyme activity is very low and thus there appears to be no inhibition. The anti-cholinesterase activity in the thoracic ganglia of the DDT treated flies showed the maximum inhibition after 24 hours i.e., 86·4%, but after 2 and 4 hours 56·7% and 57·7% respectively.

The effect of DDT on the acetylcholinesterase enzyme in the house flies is a very significant fact and it is very much pronounced in the thoracic ganglia.

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THE PENETRATION OF METHOXYCHLOR IN *MUSCA DOMESTICA NEBULO* FABRICIUS WHEN TOPICALLY APPLIED

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Very little attention has been given to Methoxychlor to study its penetration into the insect body. The recent work on the intoxication, detoxication, transference, distribution and excretion of DDT in various tissues of house flies has been reviewed (3). It is already well known that Methoxychlor is soon excreted from the body. The present investigations have been undertaken to determine the rate of penetration and detoxication in the body of *Musca domestica nebulo* Fabricius.

Microdetermination of Methoxychlor in flies was carried out by a colorimetric method (2, 1). For each experiment 50 flies of 4-5 days old were employed. The transmittancy was determined at 540μ. Each fly was treated with 5 gamma of pure methoxychlor.

Results have indicated that just after the application, 60 gamma penetrate into the body of 100 flies to which have been applied 500 gamma of Methoxychlor externally, while 440 gamma is recoverable from the external washings. In the 2nd, 3rd, 4th and 5th hours after topical application, the quantities of Methoxychlor recoverable from the external washings are 172, 256, 292, 292 and 292 gamma respectively showing thereby that the maximum penetration takes place within the fiist three hours. The quantity in gamma of Methoxychlor recovered from within the bodies of the flies after 0, 1, 2, 3, 4 and 5 hours of application are 0, 11, 12, 14, 13 and 14 gamma respectively. The maximum penetration of the Methoxychlor takes place within three hours of the topical application. The quantities in gamma of Methoxychlor which could not be accounted for are 60 gamma at 0 hours, 161 gamma after 1st hour, 244 gamma after 2nd hour and 278 gamma each after 3rd hour, 4th and 5th hour. These quantities appear to be detoxified inside the body of the flies into non-toxic products, which, however, could not be detected by the colorimetric method.

It is interesting to observe that the Methoxychlor begins to detoxify inside the body of the house fly just after its penetration. Only very small quantities i.e., 11-14 gamma are recoverable from their bodies. This is one of the reasons why Methoxychlor cannot be very effective and toxic to insects since the detoxification of this insecticide is at a very high rate.

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CARBAMATE INSECTICIDES

STRUCTURE AND INSECTICIDAL ACTIVITY OF HETEROCYCLIC CARBAMATES

H. Gysin

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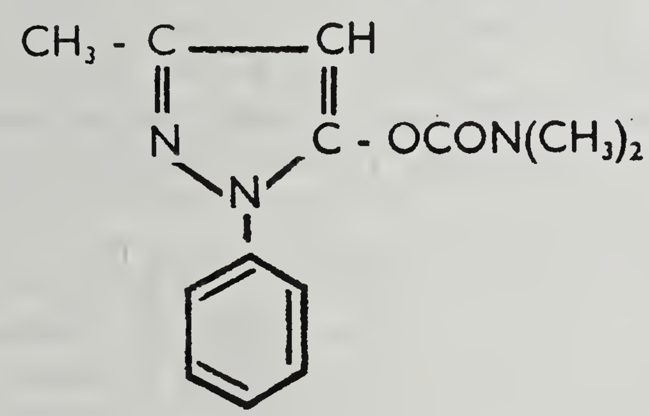
When it became evident that the dimethyl carbamate of 5,5-dimethyl-dihydroresorcinol had an insecticidal activity against houseflies (including strains resistant to chlorinated hydrocarbons), a systematic study was made in the Geigy Research Laboratories to synthesize and test a large number of cyclo-aliphatic and especially heterocyclic carbamates. In the course of these studies it could be shown that structural changes in the cycloaliphatic and heterocyclic ring systems respectively are of secondary importance only. Changes of the amines of the carbamate moiety, however, are of a very pronounced nature. In addition to the dimethyl carbamates only the mono-methyl derivatives have a strong insecticidal activity. Methyl-ethyl carbamates and all other higher homologues derived from other aliphatic primary or secondary amines have a much lower insecticidal activity. The only other carbamates showing some activity are the piperidyl carbamates of several heterocyclic enols.

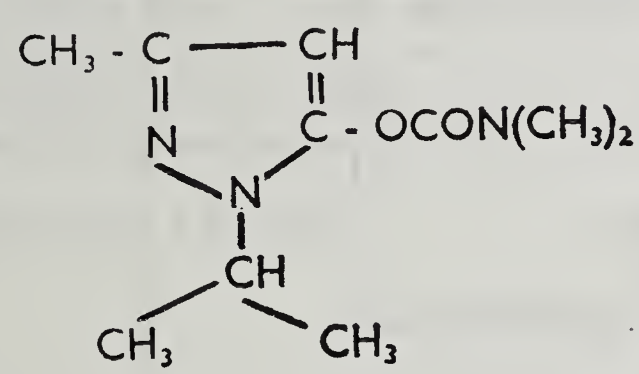
Among the heterocyclic dimethyl carbamates the following compounds were or are being used commercially today:

1. Pyrolan



which was used especially for fly-control in Switzerland before phosphates with low toxicity such as Malathion and Diazinon were commercialised.

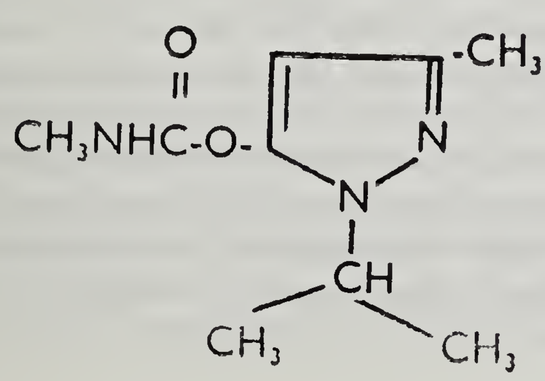
2. Isolan



which proved to be a very good systemic aphicide. Its use is limited, however, due to its high mammalian toxicity, its low persistency and its relatively small spectrum of activity.

The monomethyl-analogue of Isolan

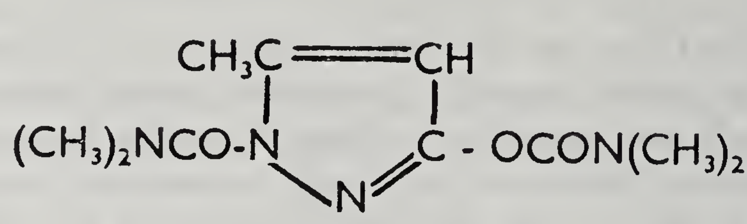
3. GS 13324



has an equally good insecticidal activity but a lower mammalian toxicity. The compound, however, is like other mono-methyl carbamates of heterocyclic enols too unstable for a practical use.

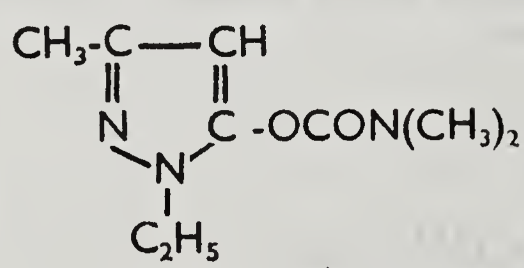
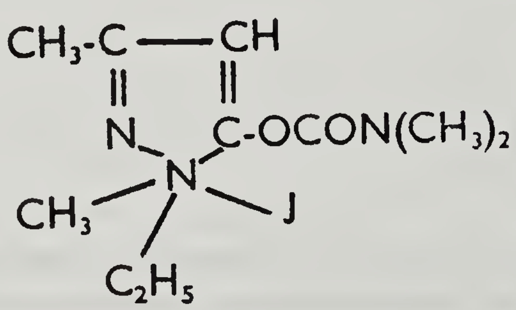
Using 3-methylpyrazolone as a starting material, it is possible to get a 2-dimethylcarbamyl-3-methyl-pyrazolyl-(5)-dimethylcarbamate. This compound known under the common name

4. Dimetilan



is used today in various formulations for fly control. The compound is active against the most polyvalent resistant fly strains which can no more be controlled by either chlorinated hydrocarbons or phosphates. The activity of Dimetilan in form of sugar preparations is primarily that of a stomach poison. The fly bands, disks, blotters etc. which are impregnated with Dimetilan plus sugar kept their full activity over a long period of time and attempts to select Dimetilan-resistant strains did not lead to any appreciable decrease of sensitivity after 50 generations.

The insecticidally active dimethyl carbamates of the heterocyclic as well as of the cycloaliphatic series are strong cholinesterase inhibitors. The mode of action of the carbamates discussed resembles to that of the phosphates. Active representatives of both categories are strong cholinesterase inhibitors. It could be shown that by quaternisation of dimethyl carbamates of the Isolan-type the inhibition of pseudocholinesterase as well as that of red blood cell cholinesterase could be considerably increased while the insecticidal activity was very remarkably decreased:

		Pseudo cholin-esterase	*Cholin-esterase*	*LD* 50 *Mice per os mg/kg*	*Effect on Musca domest.* 100% *k.o. after minutes*
G 23224		$4{\cdot}1 \times 10^{-6}$	$9{\cdot}4 \times 10^{-6}$	6	10 mg: 4 1 mg: 6
G 25255		$2{\cdot}8 \times 10^{-8}$	$2{\cdot}65 \times 10^{-8}$	21	10 mg: 88 1 mg: over 160
Eserin		$2{\cdot}7 \times 10_{-2}$	$8{\cdot}1 \times 10_{-2}$	ca. 1	no activity

The cholinesterase inhibition, therefore, cannot be the only reason for the insecticidal activity of the carbamates discussed. The stability of the carbamates in the presence of enzyme systems seems to be of decisive importance for the interference with the enzymes.

Very little is known about the fate of heterocyclic dimethyl carbamates. Although hydrolysis may be the most important pathway of the metabolism of heterocyclic dimethyl carbamates the oxidation of the intact carbamates in the heterocyclic ring cannot be excluded. It is not fully elucidated yet whether a demethylation of Isolan and the like takes place before any oxidation or hydrolysis occurs.

RELATIONSHIPS BETWEEN SOME PHYSICAL AND CHEMICAL PROPERTIES OF SUBSTITUTED PHENYL N-METHYL CARBAMATES AND THEIR RESIDUAL ACTION

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An insecticide which is intended for the control of mosquitos by the residual spraying of houses should possess certain properties. These are high intrinsic toxicity; high contact toxicity; chemical and physical properties which permit efficient formulation and application and promote low volatility and stability in the spray residues; and low mammalian toxicity.

The substituted-phenyl N-methyl carbamates are a group of compounds which contain insecticides already in commercial production and are very suitable for laboratory investigations of the various factors which influence their efficiency because of ease of preparation and purification.

They show a very wide range of intrinsic toxicities to the mosquitos, *Anopheles stephensi* and *Aedes aegypti* as measured by topical application in solution. Highest toxicities are associated with single alkyl groups at the 2 and 3 positions on the phenyl ring with a maximum when the alkyl group is 3-isopropyl. Almost as effective are compounds where several small groups such as methyl and methylthio occur at the 3, 4 and 5 positions.

High intrinsic toxicity is not necessarily an indication that a compound will be an effective contact insecticide. Tests in which mosquitos have been exposed to spray residues show that compounds with fewer and smaller substituents than the optimum for intrinsic toxicity can be very good contact poisons while others which are very effective when helped into the insect with a solvent cannot penetrate the cuticle by themselves. Measurements of solubility in n-hexane, used as a model for the wax layer of the cuticle, and of distribution coefficients between hexane and water do not yield any definite clues about the reasons for the very variable contact properties except that the poorest compounds tend to have low hexane solubilities.

These compounds also vary widely in volatility and it is perhaps unfortunate that the contact toxicity decreases as molecular size and the number of substituents, factors which promote long residual life, increase. However, there are a few compounds which retain an adequate contact action, even though it may not be at the maximum for the series, and possess very satisfactory residual properties of a similar order to those of DDT and dieldrin. As a group these carbamates are sorbed very readily by dried soils and only the most toxic ones on the least sorptive soils continue to give satisfactory kills of resting insects.

The carbamates are chemically stable on most surfaces and the only material commonly encountered in buildings on which they will not persist is limewash.

Probably the optimum balance between effective contact action and long life has been reached in this group of esters and improvements should be sought in the ratio of mammal-to-insect toxicity.

ZUR WIRKSAMKEIT VON EINIGEN PHOSPHORSÄUREESTERN UND CARBAMATEN AUF STUBENFLIEGEN (*MUSCA DOMESTICA*) VERSCHIEDEN EMPFINDLICHER STÄMME

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Um zu prüfen, ob Schädlingsbekämpfungsmittel auf neuer Wirkstoffbasis gute insektizide Eigenschaften auch gegen resistente Fliegen aufweisen, wird über Versuche mit neueren Sprühmitteln und über ihre graphische Auswertung berichtet. Handelsfertige Sprühmittel, Emulsionskonzentrate und Spritzpulver wurden in den handelsüblichen Konzentrationen auf Filterpapiere gesprüht und die aufgetrockneten, bis zu 110 Tage alternden Beläge mit

gleichalterigen Stubenfliegen von fünf verschieden empfindlichen Stämmen besetzt. Die Fliegen wurden unter Petrischalen bzw. unter ebenso flachen Behältern mit Drahtgazedeckeln gehalten. Gewertet wurde der Eintritt der definitiven Rückenlage während einer 6-stündigen Exposition. Als Vergleichsmaßstab für das unterschiedliche Verhalten der Stämme wurde die "t 50" gewählt, d.i. die Giftwirkungszeit, in der 50% der Fliegen in irreversible Rückenlage gerieten. Die t 50-Werte wurden zunächst für einen Fliegenstamm auf einem wiederholt besetzten Belag als graphische Mittelwerte, die einer Normalverteilung unterliegen, ermittelt. Dazu wurden auf Wahrscheinlichkeitspapier auf der Ordinate die Logarithmen der Summenprozente der in Rückenlage gefallenen Fliegen, auf der Abszisse die Logarithmen der Giftwirkungszeiten eingetragen. Die auf die Abszissenachse heıabgeloteten Schnittpunkte der Regressionsgeraden mit der 50% KD-Linie geben die t 50-Werte. Für jeden Wirkstoffbelag gesondert wurden die Logarithmen dieser t 50-Werte für die fünf Fliegenstämme aufgetragen und durch Linien miteinander verbunden.

Auf einem Belag von 1,75 g/m² *DDT* verhielten sich z.B. Stamm LEI als der DDT-empfindlichste, ein Phosphorsäureester-resistenter Stamm PHI zugleich als der DDT-resistenteste Stamm. PHI war 16 mal DDT-unempfindlicher als LEI. Ein Lindan-resistenter Stamm U 2 sowie die Stämme CHIP und P 7, die wir als Phosphorsäureester-resistente erhielten, waren gegen DDT noch empfindlich.

Auch auf den mit den Thiophosphorsäureestern Diazinon, Fenchlorphos, Fenitrothion oder Fenthion sowie auf den mit den Carbamaten Carbaryl oder Propoxur behandelten Unterlagen verhielten sich jeweils LEI als der empfindlichste und PHI als der unempfindlichste Stamm. Die Stämme P 7, U 2 und CHIP verhielten sich intermediär. Wirkstoffe, die auf

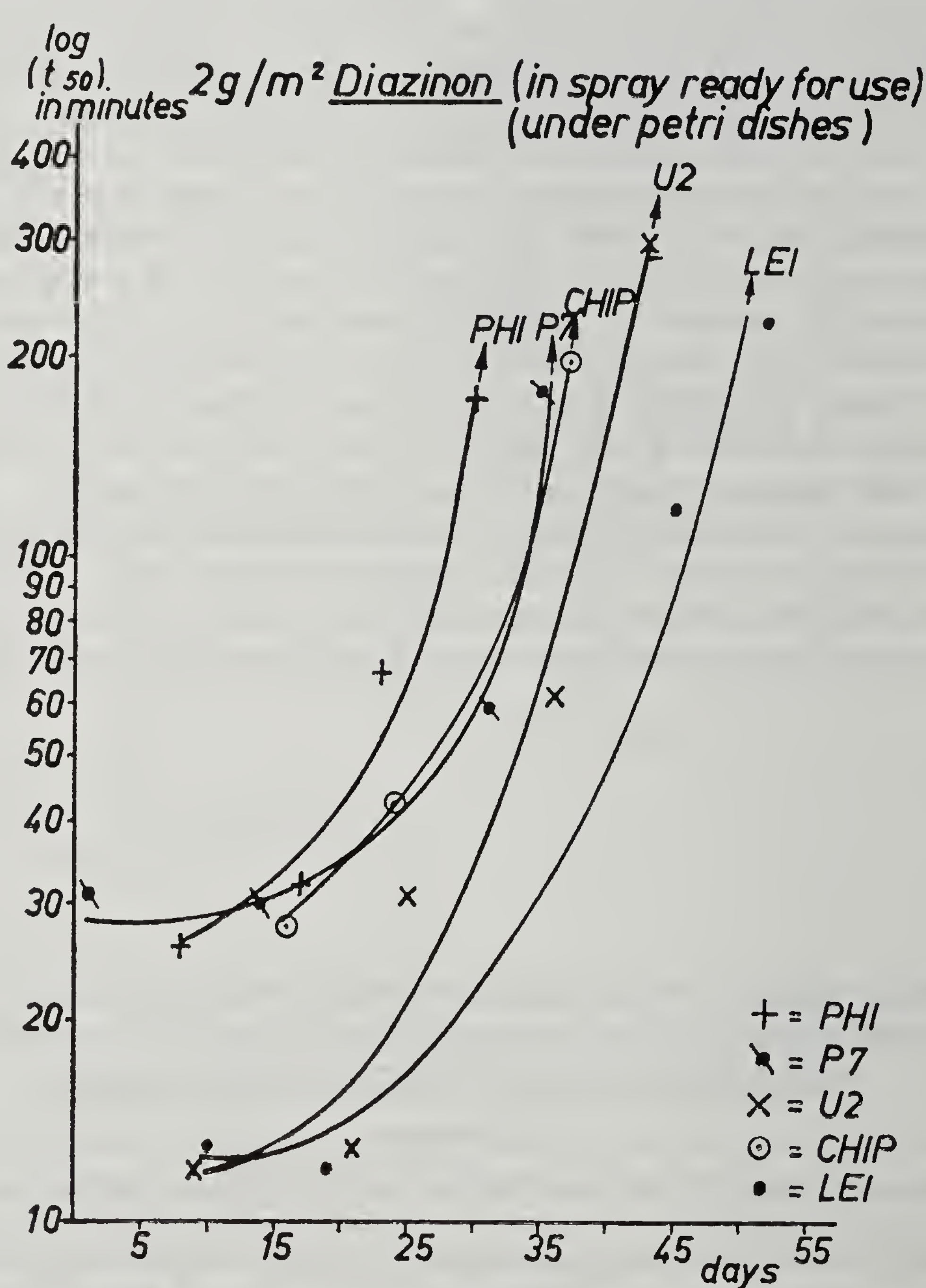

ABB. 1: Wirksamkeit eines alternden Belages von 2 g/m² Diazinon (in gebrauchsfertigem Sprühmittel; auf Filterpapier) auf Stubenfliegen fünf verschieden empfindlicher Stämme, die bei 6-stündiger Exposition unter Glasschalen gehalten wurden.

Chlorkohlenwasserstoff-resistente Fliegenstämme eine stärkere Wirkung als auf empfindliche Imagines haben, befanden sich nicht unter den geprüften Mitteln. Beläge von 1 g/m² Carbaryl bzw. Propoxur (als Emulsion) schädigten Imagines der Phosphorsäureester-resistenten Stämme PHI und CHIP nicht. Das graphische Verfahren, mit Hilfe der auf alternden Belägen ermittelten t 50-Werte die Wirksamkeit von Präparaten auf verschiedene Fliegenstämme zu zeigen, liefert recht anschauliche, aber nur relativ vergleichbare Ergebnisse.

Beispiele: (Abb. 1) Auf einer mit 2 g/m² *Diazinon* besprühten Unterlage zeigte sich bei allen Stämmen die hohe Initialtoxizität dieses Wirkstoffes: Imagines des empfindlichen Stammes LEI und des Lindan-resistenten Stammes U 2 fielen in 12 Minuten, Imagines der drei übrigen Stämme in 30 Minuten in Rückenlage. Stamm PHI, bis Ende 1962 regelmäßig mit Diazinon selektioniert, verhielt sich 1963/64 nur noch gering unempfindlicher als P 7 und CHIP. Infolge der hohen Flüchtigkeit des Wirkstoffes hat das Mittel seine Wirksamkeit eingebüßt nach 50-tägiger Alterung gegen Stamm LEI und nach 30-tägiger Alterung gegen Stamm PHI.

Abb. 2: Ein Belag von 1 g/m² *Fenthion* (als Emulsion) besitzt dagegen eine lange Wirkungsdauer infolge der Hydrolysenbeständigkeit des Wirkstoffes. Imagines des Stammes LEI wurden anfangs in 80 Minuten, bei 105-tägiger Alterung des Belages in 200 Minuten geschädigt, Imagines des unempfindlichsten Stammes PHI jeweils in einer dreimal so langen Zeit. Emulsionsbeläge von 1 g/m² Fenitrothion oder Propoxur hatten gegen empfindliche Stämme eine ähnlich lange Wirkungsdauer. Entsprechende Suspensionsbeläge auf Filterpapier waren anfangs stärker wirksam, büßten aber bei Alterung schneller an Wirksamkeit ein.

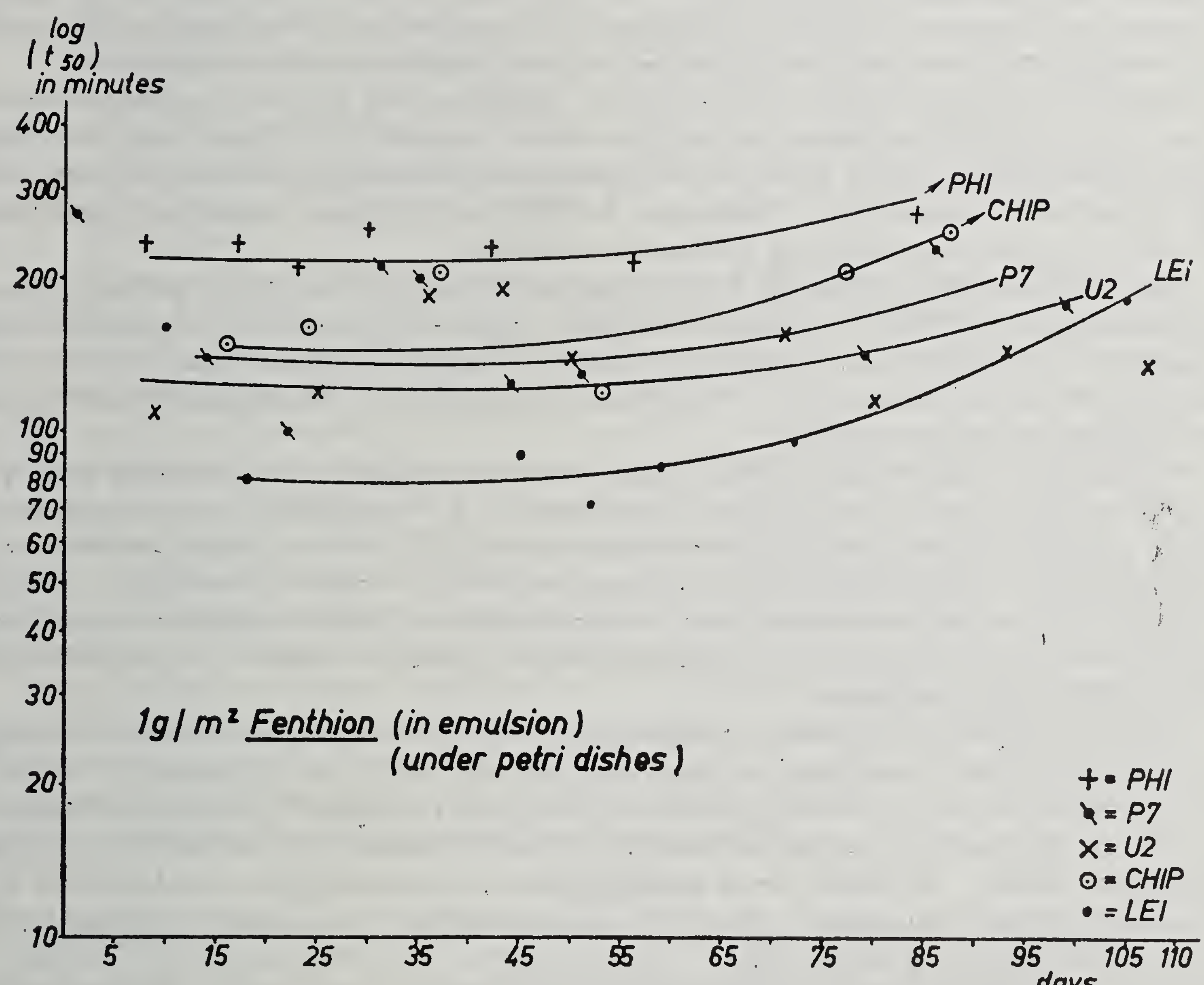

Abb. 2: Wirksamkeit eines alternden Belages von 1 g/m² Fenthion (in Emulsionspräparat; auf Filterpapier) auf Stubenfliegen fünf verschieden empfindlicher Stämme, die bei 6-stündiger Exposition unter Glasschalen gehalten wurden.

PHYSIOLOGICAL AND GENETICAL BASES OF RESISTANCE TO CARBAMATE INSECTICIDES IN HOUSE FLIES AND MOSQUITOES

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Selection of house fly strains for resistance to the carbamates Isolan (l-isopropyl-3-methyl-5-pyrazolyl dimethylcarbamate) and AC-5727 (*m*-isopropylphenyl methylcarbamate) (1) has led to the recognition of two apparently different expressions of the character of resistance. Firstly, resistance of low magnitude, as found toward the heterocyclic dimethylcarbamates Isolan and Dimetilan; the level of such resistance is well below the selection limits of the topical application method, thus, strains homogeneous for the character of resistance can be obtained. Upon release from selective pressure such strains show prolonged stability of resistance. Secondly, resistance of apparently high levels, as observed for AC-5727, and various other alkyl phenyl methylcarbamates and Sevin. Resistance to these is magnified by saturation of absorption systems, and thus its apparent extent as shown by the topical application method, does not necessarily reflect the relative efficiency of the biochemical detoxication systems. Certain of these compounds are ineffective against the heterozygous-resistant individuals (2), so that the development of a purely resistant strain by selection with these compounds is difficult, and the strain gradually reverts to susceptibility upon release from further selective pressure (3).

These types of expression of resistance to carbamates are also found in strains selected with chlorinated hydrocarbon and organophosphorus compounds.

Strains of house flies selected for resistance to the carbamates show elevated cross-resistance to chlorinated hydrocarbon and cyclodiene insecticides, such levels approaching the limits of the topical application method; they also show varying degrees of low resistance to organophosphorus compounds, resembling in this respect organophosphorus-selected strains (4).

Selection of a field strain of *Culex pipiens quinquefasciatus* for 13 generations by larval pressure with *o*-isopropoxyphenyl methylcarbamate, resulted in a 7-fold level of resistance to the selective agent and to low levels of cross-tolerance to related carbamates and certain organophosphorus compounds. Resistance to DDT and dieldrin, which pre-existed in the field strain, was intensified during carbamate selection.

Selection of *Anopheles albimanus* for 21 generations and of *Culex pipiens quinquefasciatus* for 50 generations with AC-5727 resulted in only vigor tolerance to the selective agent and to other carbamates. Dieldrin resistance, which pre-existed in *Anopheles* was lost almost entirely during selection with the carbamate (5). These results are considered encouraging from the point of view of lasting mosquito control.

Resistance to carbamates in both house flies and mosquitoes is associated with a pronounced intensification of detoxication mechanisms. A carbamate-selected strain of house flies was shown to metabolize 85% of the absorbed AC-5727 within 2 hours, while only 24% of the absorbed dose was metabolized by a susceptible strain within 3 hours (6). Larvae of the strain of *Culex* which was selected with *o*-isopropoxyphenyl methylcarbamate were found by means of C^{14}-labelled carbamate to metabolize within 3 hours 2·5 times as much carbamate as the non-selected parental strain.

Entirely independent evidence of detoxication comes from the phenomenon of synergism of carbamates by such compounds as piperonyl butoxide which are presumed to inhibit oxidative mechanisms, and tri-*o*-cresylphosphate presumed to inhibit hydrolytic mechanisms.

The genetic basis of carbamate resistance was investigated by testing the offspring of appropriate crosses. In house flies a semi-dominant, autosomal gene was found to be responsible for resistance to Isolan. However, in *Culex* resistance to *o*-isopropoxyphenyl methylcarbamate was evidently polygenic.

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CONTROL OF *ANOPHELES QUADRIMACULATUS* SAY WITH RESIDUAL APPLICATIONS OF CARBAMATE INSECTICIDES

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Since *Anopheles* mosquitoes are developing resistance to DDT and dieldrin, efforts are being made to find other insecticides to use in residual spray programs. Recent tests against adults of *Anopheles quadrimaculatus* Say indicated some methylcarbamates may be outstanding replacements for these chlorinated hydrocarbons. The dosages used are given in grams of insecticide per square meter of surface.

Laboratory tests with treated plywood panels (1, 2, 3, 5) showed that *m*-isopropylphenyl methylcarbamate was more effective than DDT, malathion, dieldrin, or fenthion. At exposures of 60-120 minutes, dosages as low as 0·01 g. usually produced 95% to 100% mortality for at least 20 weeks. Increasing the dosage reduced the exposure time required to kill, and 1 to 5 minutes on 1-g. deposits produced 97% to 100% mortality for 16 weeks. A 60-minute exposure on 1-g. deposits caused total mortality for about 1 year.

Other methylcarbamates also were effective as 1-g. deposits (2, 3). At 60-minute exposures, *o*-isopropoxyphenyl methylcarbamate produced 100% mortality for approximately 1·4 years, then lost toxicity rapidly, whereas 6-chloro-3,4-xylyl methylcarbamate and 4-(methylthio)-3,5-xylyl methylcarbamate were still causing 98% to 100% mortality approximately 1 year after treatment. 1-Naphthyl *N*-methylcarbamate (carbaryl) gave kills of 92% to 100% for 1·6 years and above 70% for another 3 months.

An outstanding characteristic of the *o*-isopropoxyphenyl, 6-chloro-3,4-xylyl, and *m*-isopropylphenyl esters was their rapidity in producing knockdown and the short contact period required for mosquitoes to acquire a lethal dose. Fresh treatments at 1 g. caused 100% knockdown within 5 minutes after exposure and even a 1-minute exposure killed all mosquitoes in 24 hours. Carbaryl and the 4-(methylthio)-3,5-xylyl ester caused no knockdown in 30 minutes.

All these compounds were applied to interiors of buildings heavily infested with mosquitoes (1, 2, 3, 4 and unpublished). Single applications of *o*-isopropoxyphenyl methylcarbamate at 2 g. produced 99% to 100% reduction throughout the first summer and at least 96% and often 99% to 100% reduction for more than 1 year. At 1 g. this compound was equally as effective throughout an 11- to 12-week period as at 2 g. A 2-g. application of *m*-isopropylphenyl methylcarbamate produced approximately the same control as 2 g. of *o*-isopropoxyphenyl methylcarbamate during the first summer; it was also quite toxic during the second year but less effective than the *o*-isopropoxyphenyl methylcarbamate. However, control in 2 of 6 buildings treated with 1-g. deposits of *m*-isopropylphenyl methylcarbamate fell below 90% on some occasions after the residues had aged 7 to 9 weeks. *m*-Isopropylphenyl methylcarbamate is now considered to be too toxic for practical use in malaria control.

When applied to infested buildings at 2 g., 6-chloro-3,4-xylyl methylcarbamate and 4-(methylthio)-3,5-xylyl methylcarbamate also produced considerable control but were less durable than the previously mentioned materials.

In contrast to laboratory results, carbaryl rarely eliminated all *Anopheles* from treated buildings after the first week and control deteriorated rapidly.

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RESISTANCE TO INSECTICIDES

EXPERIMENTS ON PHYSIOLOGIC INDUCTION OF INSECTICIDE RESISTANCE

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Immunological tolerance may be acquired, expressed in adults of higher animals, if embryonic or early life stages are exposed to appropriate antigens (1, 3). There is no reason to believe that this kind of tolerance has any parallel in insect resistance to insecticides, but the negative evidence for acquired resistance has been based on repeated exposure to insecticides late in the life cycle. It seemed desirable to test the susceptibility of adult house flies that had been exposed to DDT in their embryonic stages.

DDT applied directly to fly eggs doubtfully reaches the embryo; it is largely retained in the chorion, as determined by C_{14} labelled DDT. DDT fed in milk powder (200 ppm) to female flies becomes incorporated, along with some DDE, in ovarian eggs and continues in the emerging maggots. Thus embryonic exposure can be assured.

Group experiments on adult flies, offspring of DDT-fed parents, demonstrated that susceptibility was reduced in some cases. One test revealed a ten-fold increase in the LD_{50}. Observed inconsistencies were thought attributable to the grouping of flies in rearing and testing. Consequently, individual pairs of flies were maintained, and their progeny (all of one egg clutch) constituted the test unit. On this basis, offspring of flies fed uncontaminated milk indicated a characteristic susceptibility when challenged with 0·15 microgram DDT per fly, applied topically. On the other hand, progeny of flies fed DDT-milk segregated into two populations, one susceptible to and the other tolerant of this dosage. The two populations were essentially equal in number.

A degree of tolerance manifested in one generation thus appeared real. It remained to be tested whether this is indeed physiologically induced, or whether genotypic resistance is revealed with unusual sensitivity.

It seemed possible that the same parents could serve as their own checks. Because flies oviposit in gonotrophic cycles, it should be possible to get treated and untreated eggs from the same female. Accordingly the following combinations were established:

Cycle I.	Cycle II.
Untreated	Untreated
Untreated	Treated
Treated	Untreated
Treated	Treated

For several technical reasons, especially involving the nutritional nature of these cycles and egg maturation, few data were obtained. The possibility of physiologically acquired resistance was not excluded by this technique, however.

In the above tests, the male parent was given no special consideration as the hypothesis called for ovarian egg treatment. In a series of other tests the female flies were treated as before, but the males of a DDT-resistant strain were used exclusively. Here, the resulting progeny were all resistant to the challenging dose of DDT. This tells little except that the male effect is important. By the same method, males of the WHO specially selected susceptible strains were used with the females of the test strain fed DDT-contaminated milk. All the progeny were susceptible to the challenging dose of DDT. This immediately negates the hypothesis of physiological tolerance induced by embryonic treatment and again confirms the genetic basis of even this prompt appearance of decreased susceptibility.

What is the selective force that permits this genotypic tolerance to be revealed? The DDT-feeding is essentially non-lethal to the parents; their eggs hatch normally; there is no abnormal larval mortality nor adult emergence. There *is* a conspicuous reduction in the number of DDT-fed females capable of laying eggs and also an appreciable reduction in the number of eggs laid by those females ovipositing. Here, then is a chronic effect of DDT,

curtailing reproduction even more dramatically than that reported by Lineva (2).

It is thus concluded that with resistant genotypes present, DDT directly affects reproduction, thereby acting selectively at a celullar level, and increased tolerance of DDT becomes evident in one generation.

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THE PATTERN AND EXTENT OF DDT-RESISTANCE DEVELOPMENT IN HOUSE FLY (*MUSCA DOMESTICA* L.) STRAINS AS RELATED TO THE SEX AND STAGE EXPOSED TO THE SELECTIVE PRESSURE

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A strain of *Musca domestica* L. with no history of resistance was employed as the parental stock for the laboratory selection of DDT resistant strains using as selective forces, DDT

Table I
THE Development of DDT Resistance in House Fly Colonies Subjected to Different Forms of Selective Pressure

		Males		*Females*	
Colony	*Generation*	*LD_{50} (mg/fly)*	*Resistance Ratio*†	*LD_{50} (mg/fly)*	*Resistance Ratio*†
Par.	1	0·7		1·2	
	5	0·7		1·3	
	10	0·6		1·1	
	21	0·7		1·3	
	32	0·7		1·1	
MIP	5	8·4	12	19·2	16
	10	5·0	8	14·0	12
FIP	5	2·1	3	3·8	3
	10	7·4	11	18·2	15
$MFIP_1$	5	11·2	17	21·5	18
	7	10·7	16	20·6	17
	10	10·2	15	18·7	16
$MFIP_2$	7	6·8	10	18·1	15
	10	8·1	12	19·5	16
MFCP	5	5·4	8	12·2	10
	8	6·8	10	13·4	11
	10	8·6	13	14·4	12
MFLIP	7	7·0	10	21·5	18
	10	7·6	11	15·3	13
LIP	3	6·0	9	16·8	14
	11	7·5	11	12·8	11

$$\dagger\ \text{Resistance Ratio} \approx \frac{LD_{50}\ \text{of Pressure Colony}}{\text{Mean } LD_{50}\ \text{of Control}}$$

applied topically to the adults of each sex separately and to the adults of both sexes simultaneously. In addition DDT was incorporated into the larval medium only and also into larval medium in combination with adult treatment.

The effect of increasing the selection pressure as the strain showed increased resistance was compared with the effect of holding the selective pressure constant. (The effects of releasing the selective pressure after resistance has been established and of both releasing the selective pressure and diluting the resistant strain with equal numbers of non-resistant individuals has previously been reported (1). It is considered that the common parental stock, the carefully controlled topical dosages, and the uniform testing techniques give these experiments significance.

Table I presents a summary of the results with the parental colony (Par.); with the colony developed by applying increasing selective pressure to male adults only (MIP), to female adults only (FIP), to male and female adults in two separate trials ($MFIP_1$ and $MFIP_2$), to larvae only (LIP), to larvae and all adults (MFLIP); and with the colony developed by applying a constant selective pressure to male and female adults (MFCP).

All colonies under pressure developed resistance by generation 5. However, the colony in which females only were treated developed its resistance much more slowly, the level being much lower than the others at generation 5. By generation 10 all were resistant although some difference in levels of resistance occurred. When the selective pressure was released, resistance dropped slowly unless the colony was diluted, in which case the resistance dropped within three generations (1). Under continued selective pressure the resistance, having reached a peak, remained relatively constant.

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INVESTIGATION OF THE BIOCHEMISTRY OF FLUOROACETATE RESISTANCE IN HOUSE FLIES

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A fluoroacetate resistant fly strain has been selected in our laboratory (4). Fluoroacetate, after conversion to fluorocitrate in animal tissues *in vivo* and *in vitro*, inhibits aconitase, thus causing accumulation of citrate (3). The purpose of this study was to determine how the resistant strain overcomes the toxic effect of fluoroacetate.

The following house fly *Musca domestica* L. strains were used: "S" the insecticide susceptible Stauffer strain; and "F", selected from "S" for fluoroacetate resistance. Citric acid was determined by a modification of the method of Natelson et al. (2); pyruvic and other keto acids by a modification of the method of Friedemann and Haugen (1). The respiration of fly sarcosomes was measured according to van den Bergh and Slater (5). Particles were isolated by the method of van den Bergh and Slater (5), modified by the addition of bovine serum albumine to the isolation medium.

Feeding of fluoroacetate to flies of both strains caused accumulation of citrate. The rate of accumulation was higher in the susceptible strain. No significant increase could be detected in the resistant strain three hours after feeding, while in the susceptible strain citrate accumulation nearly reached its peak at this time. In both strains the high levels of citric acid after feeding of fluoroacetate persisted for at least 6 to 7 days. The feeding of citrate itself caused no mortality in either strains.

The pyruvate contents of flies of both strains increased significantly 1 hour after the feeding of fluoroacetate. The level of accumulation being dependent on the quantity of fluoroacetate fed. This rapid accumulation indicates that fluoroacetate is able to penetrate cells of both strains.

Fluoroacetate at a concentration of 10^{-3}M to 10^{-4}M inhibits sarcosome respiration on

pyruvate with malate, on fumarate, and on malate alone. The initial rates of succinate oxidation were not affected. It is therefore suggested that the inhibition of oxidation by fluoroacetate at these high concentrations occurs at a stage which is not the aconitase one. This is also indicated by the pyruvate accumulation encountered in the *in vivo* experiments.

In washed mitochondria no accumulation of citrate could be detected, when the substrate was either fumarate, malate, or pyruvate with malate. Unwashed mitochondria incubated with fluoroacetate, gave a two-fold increase in citrate contents on fumarate or on malate, while there was no citrate accumulation on pyruvate with malate. It appears that pyruvate competes with fluoroacetyl CO-A for the condensing enzyme, through a rapid supply of acetyl CO-A, thus preventing the formation of fluorocitrate and the accumulation of citrate. If these findings are corroborated by *in vivo* experiments, then it could be considered likely, that the fluoroacetate resistance of our fly strain is correlated with the rate of pyruvate production.

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RELATIONSHIP OF *IN VITRO* HYDROXYLATION TO RESISTANCE IN *MUSCA DOMESTICA* AND *PHORMIA REGINA*

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Microsomes prepared from three pesticide resistant and one susceptible housefly strain have been compared with those of the blowfly (*P. regina*) in the hydroxylation of naphthalene^{-1}-C-14. The microsomes are prepared by homogenizing the insects in a Waring blender in 0·15M KCl. After a 30 second homogenization of 20 grams of insects in 150 mls of KCl, the homogenate is separated by stepwise centrifugation at 0°C. to yield a microsomal pellet sedimenting at 100,000 × g. Microsomes equivalent to 15 mg protein (biuret method) are incubated at 34°C. with C-14-naphthalene and a NADPH generating system at pH 8·2 (tris buffer). After 30 minutes the reaction products are extracted with ether and measured radiometrically.

The products of the hydroxylating reactions are primarily l-naphthol and 1:2 dihydroxy 1:2 dihydro naphthalene with smaller quantities present as more polar products (thought to be conjugates).

The reactions are inhibited by the pyrethrin synergists. Inhibitory concentrations (IN_{50}) range from 10^{-5}M for isosafrole, safrole, and piperonyl cyclonene to 10^{-3}M for piperonylic acid. The well-known inhibitor of biological oxidations, SKF-525A, was also effective at 10^{-3}M. A total of 15 methylenedioxyphenyl compounds was studied. *In vivo* tests with female houseflies exposed to naphthalene vapors confirmed the synergism.

The microsome experiments involved male and female insects of different ages up to 14 days after emergence. No significant sex differences in hydroxylation were noted but age differences were great. Ten day old flies possess microsomal tissue approximately twenty times the activity of two day old insects.

In comparing microsomes from the two species, *P. regina* and *M. domestica*, a significant difference in hydroxylating activity was found. Blowfly microsomes, prepared in the same way as those of houseflies, hydroxylated only one-third as much naphthalene as the least active housefly preparation (Milan S, standard reference strain) and one-tenth as much as the most active housefly preparation (Naphthalene R strain). Attempts to improve the activity of the blowfly microsomes by increasing the microsomal level, doubling co-factors, addition of

metal ions, and addition of the soluble fraction from housefly or blowfly preparations were all unsuccessful. Absence of an inhibitor in the blowfly preparations was proven in tests with mixtures of blowfly and housefly microsomes in which case normal housefly level hydroxylation was attained.

Dosage mortality experiments measured the susceptibility of the blowflies and of the four strains of houseflies to naphthalene vapors and to topically applied DDT and dieldrin. As expected from the *in vitro* studies the blowflies were highly susceptible to the three toxicants. The Naphthalene R strain was highly resistant to dieldrin and moderately resistant to DDT. The microsomal hydroxylating activity of the four housefly strains also correlated with their susceptibility to the three compounds.

The results support the idea that hydroxylation is an important biochemical reaction in the detoxication of such insecticides as DDT and dieldrin. The synergist studies indicate that this biochemical reaction (hydroxylation) is also important in the action of the methylenedioxyphenyl synergists.

METABOLISM OF PARATHION IN RESISTANT AND SUSCEPTIBLE RICE STEM BORER

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Parathion was first introduced into Japan in 1952 to control rice stem borer (*Chilo suppressalis* Walker), one of the most important pests of rice plant. In 1960, resistance was first observed in paddy fields in the Shikoku district where parathion had been applied very intensively. Field application of parathion for about eighteen generations of the borer has increased LD50 seventeen to forty times the normal. It was shown that parathion resistant borer was also resistant to paraoxon. No difference of activities of cholinesterase and aliesterase or susceptibilities of these enzymes to parathion and paraoxon were observed between the resistant and susceptible strains.

Studies on the metabolism of parathion in the susceptible and resistant strains were made with radioactive p^{32} labelled parathion. We were able to study the metabolic fate of parathion which was applied topically on the larvae. Parathion was absorbed and distributed in the tissues of the borer and subjected to the diverse biochemical processes including activation and detoxication. Parathion and its metabolites can be isolated quantitavively from homogenized larvae by partitioning between chloroform and water. The chloroform extract contains parathion, paraoxon, and their metabolites which are still active, and the water extract contains degraded substances.

Parathion resistance appears to be metabolic due to differences in rates of degradation, and in resistant strains much more parathion is converted to nontoxic derivatives, which were excreted rapidly.

To elucidate the metabolism of parathion in resistant and susceptible borers, the final separation and identification of the chloroform extract was performed on a silicon impregnated reverse phase chromatography after the method of Metcalf and March (1953). Separation and identification of the water extract was made with ion exchange chromatography after the method of Ploff and Casida (1958). Radioactivity of each metabolite was measured. In the susceptible strain, much more parathion remained unchanged, and in the resistant strains much more parathion was hydrolized and degraded into nontoxic substances. Parathion resistance is related to detoxication mechanisms.

Detoxication of p^{32} parathion and paraoxon by the tissues of the resistant and susceptible borer *in vitro* was examined. Results showed that blood has the most important role in detoxication of parathion and paraoxon in the resistant strains.

Although differences have been found between the resistant and susceptible strains of borer with regard to the zymograms of esterases separated and revealed by means of the thin

layer agar gel electrophoresis, there is no conclusive evidence that such differences may account for resistance to parathion.

Parathion resistant borers showed no cross-resistance to methyl parathion and EPN. There was no significant difference in the rate of destruction of p^{32} methyl parathion between resistant and susceptible strains. Thus, parathion resistance does not exhibit a group resistance pattern as does chlorinated hydrocarbon resistance, and the mechanism of resistance seems to be related to slight structural changes in the organophosphorus insecticides.

Resistance to parathion is relatively unstable, and on removal of selection pressure, resistant borers decrease their detoxication ability and become susceptible again in six generations.

RESISTANCE TO INSECTICIDES IN COCKROACHES

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Resistance to chlordane in a natural population of the German cockroach first occurred in Texas, U.S.A., in late 1951. Later studies and surveys revealed the existence of resistance to chlordane, dieldrin, and lindane in many populations in the southern and southeastern areas of the United States. Today resistance is widespread ovei the U.S. but, curiously enough, chlordane is still effectively used in some areas. Resistance to chlordane, dieldrin, and lindane has now been confirmed in German cockroach populations from the Panama Canal Zone, Trinidad, Germany, France, England, Canada, Puerto Rico, and the American Tropics.

Resistance to DDT in natural populations of the German cockroach has been reported from Trinidad, Germany, France, England, and the American Tropics. Apparently, the only DDT-resistant strain in the U.S. was produced by selection in the laboratory.

Low to moderate resistance to diazinon in two field strains of the German cockroach from Kentucky, U.S.A., was found in 1959. Low-level resistance to diazinon, malathion, Entex, and pyrethrins was found in four field strains from Texas in late 1963. It was shown as early as 1959 that resistance to malathion could be induced through laboratory selection.

Apparently, resistance has not yet occurred in other species of cockroaches, except for one report of resistance in the Oriental cockroach to DDT and chlordane in Europe.

Resistance to DDT is thought to be inherited as a monofactorial autosomal trait and to be essentially recessive. Resistance to cyclodiene derived insecticides is thought to be carried primarily by one factor on the autosomes, but the F_1 hybrid is intermediate between the parental strains.

Resistance to chlorinated hydrocarbons is rather specific within groups; however DDT imparts some cross-resistance to Sevin. Resistance to malathion is specific, but apparently selection with diazinon induces some tolerance to many organo-phosphates.

Loss of resistance to chlordane is gradual with $12\times$ remaining in the females after 25 generations of no selection. Loss of resistance to DDT is very rapid with only $4\times$ remaining in females after 12 generations. A moderately rapid loss of resistance to malathion occurs immediately following release of selection pressure, but considerable resistance ($11\times$ to $36\times$) remains after 10 generations.

DDT-resistant males and females are smaller than normal ones in total length, head width, and pronotal length and width. Chlordane-resistant roaches are smaller than normal ones only in total length and head width; lindane-resistant males and females are smaller than normal ones in head width, and pronotal length and width.

DDT-resistant roaches have shorter incubation period, but longer nymphal developmental period and greater longevity of females than those from the normal strain. Chlordane-resistant roaches differ from normal ones only in greater female longevity. Lindane-resistant roaches have longer nymphal period and greater female longevity than normal roaches.

CONTRASTING SUSCEPTIBILITIES TO MALATHION IN HIDE BEETLES (*DERMESTES*) AND THEIR INTERPRETATION

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Studies on the susceptibility of larvae of *Dermestes maculatus* DeG. and *D. lardarius* L. to insecticides applied topically in ethyl cellosolve, showed that fenitrothion, fenthion and dicapthon were more effective than pyrethrins, DDT, coumaphos and butonate. Lindane and diazinon were of intermediate effectiveness.

The LD 50 for malathion against *D. maculatus* was 10 × that for this compound against *D. lardarius*. Compared to the latter *D. maculatus* was also slightly more tolerant of malaoxon and dimethoate, but not of diethyl malathion, nor of several other organophosphorus insecticides. The spectrum of tolerance shown by *D. maculatus* in comparison to *D. lardarius* is similar to the resistance spectra of the malathion-resistant strains of *Culex tarsalis* (Coq.), *Musca domestica* L. and *Chrysomya putoria* (Wied.) studied by Plapp *et al.* (1963, J. econ. Ent. 56: 643-9) and Busvine *et al.* (1963, Bull. ent. Res. 54: 589-600).

The malathion-resistant strain of *Culex* has been shown to detoxify malathion by hydrolysis of the carboxyester groups (Matsumura and Brown 1961, J. econ. Ent. 53: 777-81). Similar detoxification is likely in the malathion-resistant strains of *Chrysomya* and *Musca*, since in the malathion-resistant strains of all three flies malathion has been reported to be synergised by EPN, triorthocresyl phosphate or triphenyl phosphate. In contrast, these compounds are relatively or completely ineffective synergists for malathion against the susceptible strains of these flies.

Triphenyl phosphate synergised malathion against *Dermestes maculatus*. The factor of synergism was × 12 when the ratio of insecticide to synergist was one to twenty. In contrast, the same compound slightly antagonised malathion against *D. lardarius*. This selective synergism, coupled with the contrasting tolerances to malathion and malaoxon, was interpreted as an indication of higher carboxyesterase activity in *D. maculatus*.

The strain of *D. maculatus* used had been in culture since 1952. There was no evidence that it was a resistant strain, and another strain derived from an infested Asian cargo was found to have a similar tolerance to malathion.

Qualitative tests using triphenyl phosphate in a ratio of 10:1 with di-ethyl malathion, malaoxon, or fenthion gave no significant increase in mortality. Similar tests with coumaphos or dimethoate showed synergism, and with fenitrothion or dicapthon, antagonism. These tests were confined to *D. maculatus* and factors of synergism or antagonism were not measured.

THE EFFECT OF SOME ORGANOPHOSPHORUS INSECTICIDES ON *DERMESTES* SPP.—AN HISTOCHEMICAL STUDY

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The Gomori modification of the Koelle staining technique for cholinesterase (ChE) has been used to examine the extent of ChE inhibition in nerve cords of larvae of *Dermestes* spp. treated topically with insecticide, triphenyl phosphate, or with insecticide and triphenyl phosphate together in a ratio of 1 to 10. In all treatments ethyl cellosolve was the solvent and a total volume of 0·3 μl was applied to each larva. Estimations of ChE activity were made at various intervals, from one hour to five days after treatment, by microscopic examination of isolated, stained nerve cords.

When *D. maculatus* was treated with malathion (6 μg per individual), no inhibition of ChE was observed. However, the same dose when administered with triphenyl phosphate caused considerable inhibition, while triphenyl phosphate alone at the same dosage (60 μg per individual) produced no inhibition in this species or in two others examined (*D. ater* and *Alphitobius laevigatus*). With *Dermestes lardarius* a much lower dose of malathion (1·08 μg)

caused a high level of inhibition, but the same dose with triphenyl phosphate produced a somewhat lower level of inhibition. The marked effect of triphenyl phosphate in the production of inhibition in *D. maculatus*, and the slightly reduced inhibition observed in *D. lardarius* indicate synergism between the two compounds in the former, and slight antagonism in the latter species.

Lower concentrations of malaoxon (0·9 μg applied to *D. maculatus;* 0·18 μg to *D. lardarius*) caused very rapid inhibition of ChE in both species, but *D. maculatus* was again less susceptible than *D. lardarius.* In both species malaoxon and triphenyl phosphate produced less ChE inhibition on the same day as treatment compared with insecticide alone, indicating well-marked antagonism. After one day the degree of inhibition corresponded closely to that of the insecticide alone, showing that the antagonism was an initial effect only.

Diethyl malathion (4·5 μg for both species) was very slow in its effect and only low levels of ChE inhibition occurred. A slightly higher level of inhibition was noted in *D. maculatus* indicating that this species may be somewhat more susceptible than *D. lardarius.* There was no evidence of synergism in either species.

When both species were treated with the same dose of coumaphos (7·5 μg) there was very little difference between them in the extent of ChE inhibition. Coumaphos with triphenyl phosphate produced a higher level of inhibition in both species, but the effect was greater in *D. maculatus.* This indicates synergism, though on a smaller scale than that produced by malathion and triphenyl phosphate.

It is possible that the natural tolerance of *D. maculatus* to malathion is due to a system of carboxyesterase degradation, that is comparable to the detoxification mechanism found in malathion-resistant strains of certain Diptera. The synergism with triphenyl phosphate supports this suggestion although at present it is not fully understood what effect this compound may have on enzymatic degradation at other parts of the malathion molecule.

INSECT CONTROL—WHERE NOW?

THE FUTURE COURSE OF INSECT CONTROL

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Regulation of sale of insecticides, and of residues in foods, started soon after the use of the first commercial insecticide in the United States. This was necessary because undesirable attributes of this insecticide could not be eliminated. Increasing complexity of both insecticides and the ways in which they are used has been followed by increased regulation.

Changes now in prospect make it evident that economic entomologists must be prepared to accept many new responsibilities. These could be expanded to the degree that the entomologist prescribes treatment of specific crops on individual farms.

The obvious "solution" of development of insecticides that will avoid or minimize many problems is well under way, thanks chiefly to the European chemical industry. However, more permanent methods, with or without the use of insecticides, are highly desirable.

The present use of agricultural insecticides in the United States came about because there were insect pests, and controlling them produced more food and fiber per acre, and food not infested by insects.

Accomplishments in the control of insects without insecticides have been notable, but have been confined to a very small proportion of the serious pests. Moreover, the applications have been specific rather than general.

The combination of biological and insecticidal control has been advocated. Pickett (1) proposed minumum use of materials least toxic to enemies of insects. Stern and his colleagues (2) of California described the integrated control concept. This proposed to use insecticides in such a way that natural control is supplemented rather than supplanted. They stated frankly that it is not a panacea.

Further sound development of these concepts is desirable. But it is obvious that successful application demands a high degree of knowledge of biology of pests and parasites, of population potentials and of effects of insecticides.

Thus, regardless of the exact method of insect control developed, there will be a need for specialists in insect control. They must be proficient in all ways of insect control, and not committed to one. They must be capable of selecting the means offering the best prospects in individual cases.

As far as the research is concerned, it matters little whether effective control comes from the studies of specialists in insect pathology, biological control, toxicology, or whatever. It is most important that solutions be found, and to divert efforts to discussions as to how to find them postpones the finding.

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RECENT STUDIES ON THE BASES OF SELECTIVITY IN INSECTICIDES

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One of the factors governing the design and selection of new insecticides is appropriate selective toxicity; for instance, one appropriate pattern is that of wide-spectrum insecticidal action with negligible toxicity to vertebrates. For several years a part of our work has consisted of exploring the biochemical and physiological causes for various patterns of selectivity, in order to provide a basis for the design of new compounds. In this exploration we have encountered most of the mechanisms which had been considered plausible *a priori*. Some recent examples are as follows:

(*a*) The earlier finding that the low toxicity of malathion to mammals is due to rapid cleavage of the $COOCH_3$ group, has been extended to malathion-resistant houseflies and *Culex* mosquitos; their resistance was profoundly different towards malathion analogs where the CH_3 of the $COOCH_3$ was replaced by other alkyl groups.

(*b*) Dimethoate shows profound selective toxicity amongst vertebrate as well as insect species. In the vertebrates, the variation is caused by differences in extent of degradation in liver; the predominance of POC or $CONHCH_3$ cleavage varies greatly but independently of the extent of degradation. In insects, differences in degradation are fairly small whereas differences in activation and cuticle penetration are large; but the principal factor in selectivity appears to be in the susceptibility of the cholinesterases.

(*c*) Caution is needed in attributing selectivity to differences in hydrolytic cleavage, in view of the unexpected finding that a new compound (Du Pont 3323-57), which can be viewed as a cleavage product, is a potent anticholinesterase. Cleavage of its parent would therefore not be a detoxification.

(*d*) Large differences in sensitivity of cholinesterase have been observed, e.g. between house fly and bovine enzyme for Ruelene; between house fly and bee for the isopropyl analog of paraoxon; and between amphibia and mammals for a variety of anticholinesterases. In the one case where such a situation has been fairly extensively explored, it has not been easy to

affirm positively a direct connection between differences in cholinesterase sensitivity and selective toxicity.

(*e*) An interesting case of two strains of organophosphate-resistant spider mite having evolved different mechanisms of resistance has been observed. Smissaert had reported that the Leverkusen strain had developed a relatively insensitive cholinesterase. We have confirmed this, but find that the Blauvelt strain has a normal cholinesterase and an enhanced ability to degrade organophosphates.

(*f*) The insensitivity of milkweed bug eggs to parathion vapour has been explored and appears to be due to retention of the compound in the epicuticular wax. The embryo receives negligible amounts of parathion until hatching. Of many compounds tested, only dipterex and DDVP had significant ovicidal action for this insect, and it was shown for DDVP that large quantities penetrate to the embryo. Presumably the difference between parathion and DDVP is largely due to their difference in polarity.

In conclusion, the above and other studies have revealed a multiplicity of mechanisms of selectivity, and provide grounds for hope that in spite of the diverse practical requirements for particular patterns of selectivity, compounds demonstrating such patterns can be prepared.

(Note: the findings described are based on collaborative work with Drs. Dauterman, Matsumura and Zschintzsch and Messrs. Aharoni and Uchida).

THE CHEMISTRY AND BIOLOGICAL ACTIVITY OF THE INSECT SEX ATTRACTANTS

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Many entomologists believe that insects have persisted in great numbers because of their very high reproductive potential. This potential is based on the ability of the opposite sexes to find each other and mate. An important, if not essential, link of this process is the sex attractant, usually released by the female to lure the male. Detected by the insect in fantastically minute amounts, these substances are the most potent physiologically active materials known today. For example, the male American cockroach, *Periplaneta americana*, has been found to respond to 10^{-14} microgram, or about 30 molecules, of the female lure, which has been identified by chemists of this Department as 2,2-dimethyl-3-isopropylidenecyclopropyl propionate (1). This attractant was obtained as 12·2 milligrams of a liquid from 10,000 live female roaches over a 9-month period; it elicits typical intense excitement, wing raising, and copulatory attempts in males. Other reports tell of the gypsy moth, *Porthetria dispar*, being trapped from distances greater than 2 miles, with average flights ranging from $\frac{1}{4}$ to $\frac{1}{2}$ mile. One caged female of the introduced pine sawfly, *Diprion similis*, attracted well over 11,000 males in the field (2).

The prevalence of sex attractants in the insect world is still one of nature's best kept secrets. The more obvious instances of insects attracting mates were discovered by observing males responding to caged or immobilized females, or vice versa. Such observations are as yet comparatively few, but there is no doubt that sex lures are widespread among insect species. Up to the present time, sex attractants have been demonstrated in approximately 200 insect species, and the study of these substances has grown by leaps and bounds within the past 4 years. This is true not only because they are fascinating materials structurally and physiologically, but because the sex attractants, although essential for reproduction of the species, may be used to control and possibly eradicate them.

Sex attractants among insects of the order Lepidoptera have received the most detailed chemical study to date. This work has centered mainly on the attractants of the silkworm moth, *Bombyx mori*, and the gypsy moth. In both species the attractant is formed in the lateral glands of the virgin female abdomen. The female is able to protrude and retract these glands, and in this manner she regulates the release of the attractant.

"Bombykol", the sex attractant of the female silkworm moth, was isolated as 7 milligrams

of an oily liquid from 500,000 virgin females. It was identified in 1960 as *trans*-10,*cis*-12-hexadecadien-1-ol (I) and its four possible geometrical isomers have been synthesized (3). These isomers show the following attractiveness to male silkworm moths (micrograms/ml.) in laboratory tests: *cis*-10,*cis*-12, 1; *cis*-10,*trans*-12, 10^{-4}; *trans*-10,*cis*-12 (bombykol), 10^{-12}; *trans*-10,*trans*-12, 10 (4). A whirring vibration of the wings and typical circling dance are elicited in the male by an active compound.

After 30 years of study, the gypsy moth sex attractant was isolated, characterized, and synthesized in 1960 (5). To isolate the attractant, it was necessary to clip the last two abdominal segments of many virgin female moths, separate the neutral fraction from a benzene extract of the abdomens, and either chromatograph by a tedious process on adsorbent columns, or what is more satisfactory, dissolve the neutral fraction in acetone, precipitate out the inactive solids, and subject the yellow oil to paper chromatography. Of the five spots obtained, only one was attractive to males, and this was separated into a highly attractive colorless liquid (the major attractant) and a solid of much lower activity. A total of 20 milligrams of pure major attractant was isolated from 500,000 females; its structure has been identified as *dextro*-10-acetoxy-*cis*-7-hexadecen-1-ol (IIa). It elicits a positive response from males (excitement, curving of the abdomen, and copulatory attempts) at 10^{-12} microgram in the laboratory and 10^{-7} microgram in the field.

Characterization of the natural gypsy moth attractant resulted in the synthesis of a homolog, *dextro*-12-acetoxy-*cis*-9-octadecen-1-ol (IIb), which has been designated "gyplure" (6). Readily available at low cost, gyplure has the biological activity shown in Table I, which also gives the activity of another homolog (IIc) and of several related materials (7).

$$CH_3(CH_2)_2CH\overset{c}{=}CHCH\overset{t}{=}CH(CH_2)_8CH_2OH \qquad \mathrm{I}$$

$$CH_3(CH_2)_5\underset{\substack{|\\ OCCH_2\\ \|\\ O}}{CH}CH_2CH\overset{c}{=}CH(CH_2)nCH_2OH$$

IIa. n = 5
IIb. n = 7 (gyplure)
IIc. n = 9

TABLE I
Comparative Attractancy of Gyplure and Its Homologs to Male Gypsy Moths

Compound	Attractancy, μg. Laboratory	Field
d-IIa (natural)	10^{-12}	10^{-7}
dl-IIa (synthetic)	10^{-12}	10^{-6}
l-IIa (synthetic)	10^{-12}	10^{-6}
d-IIa (synthetic)	10^{-12}	10^{-7}
d-IIb (*cis*-gyplure)	10^{-12}	10^{-5}
d-IIb (*trans*-gyplure)	10^{4}	$2{\cdot}5 \times 10^{5}$
d-IIc	10^{-2}	10

Failure to control rigidly production conditions in the large-scale manufacture of gyplure may render the final product unattractive to male gypsy moths; various proportions of structurally related unattractive batches of gyplure have occasionally been found to contain 9 or 10 masking contaminants. Adsorption and gas chromatographic methods have just been developed by our chemists for determining the content of *cis*-gyplure in its samples, as well as for separating the *cis* isomer from its contaminants (8).

The structural similarity between bombykol and the gypsy moth sex attractant is remarkable. Both compounds are 16-carbon straight-chain, unsaturated primary alcohols, and are thus neutral lipid (fat-soluble) substances. Chemical investigation, now in progress, of the

sex attractants of a number of economically important pests shows the existence of a close structural interrelationship between these substances that may be general for the Lepidoptera. Work in our laboratories, as yet unpublished, shows that the sex attractants of the pink bollworm moth (*Pectinophora gossypiella*), tobacco hornworm moth (*Protoparce sexta*), and southern armyworm moth (*Prodenia eridania*) all possess neutral, aliphatic, long-chain structures. In addition, Egyptian investigators have recently shown that the sex attractant of the cotton leafworm moth (*Prodenia litura*) is a neutral lipid probably possessing a primary alcohol group (9).

The gypsy moth is an excellent example of an insect whose sex attractant may be used for survey and possibly for control. Males fly into the wind and pick up the scent as they approach the nonflying females. For many years, the U.S. Department of Agriculture made use of a benzene extract of the abdominal tips in field traps to locate infested areas and determine the size of the infestation by the numbers of males caught in these traps. Gyplure has replaced this extract completely in such traps. A sex attractant can assure the early detection of an infestation before it can enlarge or spread. Control measures need be applied only to those areas where the insect is found and only as long as it continues to be present. Sex attractants may further aid in control by confusing the males to the point where location of females is prevented, or by luring large numbers of males to a toxicant or chemical sterilant.

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INSECT REPELLENTS—THEIR PRESENT USEFULNESS AND FUTURE DEVELOPMENT

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Insect repellents provide a means of protecting man and animals against many dangerous and annoying insect pests in situations where control is impractical. We have no completely satisfactory repellents. Repellents cannot compare with immunization for protection from insect-borne diseases, nor do they provide a satisfactory substitute for an effective control program in reducing the annoyance from pests. If properly used they will, however, greatly reduce the risk of infection with disease and provide a high degree of personal comfort in the presence of large numbers of bloodthirsty insects.

None of our present repellents are ideal. They have some odor, they feel oily, and they soften paint and some plastics. They must be applied at relatively massive dosages, in the range of 20 to 40 mg. per 10 cm.^{2} of skin. Even then they are effective only a few hours, most of their repellency being lost, in practical use, by their being rubbed on the clothing or other objects.

Complete protection against the entire range of biting pests requires treatment of the clothing as well as application of repellents to the skin, and the materials that are most effective for one purpose are not always suitable for the other. The better repellents are: for mosquitoes (skin and clothing applications)—deet (*N*,*N*-diethyl-*m*-toluamide), chlorodiethyl benzamide, ethyl hexanediol, dimethyl phthalate, dimethyl carbate, and Indalone (butyl 3,4-dihydro-2,2-dimethyl-4-oxo-2*H*-pyran-6-carboxylate); for ticks (clothing application)—deet, Indalone, dimethyl carbate, dimethyl phthalate, and benzyl benzoate; for fleas—deet

(skin and clothing applications) and benzyl benzoate (clothing applications only); for chiggers (larvae of Trombiculid mites)—benzyl benzoate (clothing only) or any of the mosquito repellents (skin and clothing).

Clothing can be treated most efficiently and economically by saturating the garments with a 5% emulsion of the repellent, or a 5% solution in a volatile solvent. About 2 1/2 ounces of repellent in about 3 pints of water or solvent is needed for a medium-sized outfit (jacket, trousers, and socks) of heavy cotton cloth. Application from a pressurized can is quicker and more convenient, but also more expensive.

If we are to make better use of repellents in the future, we will either have to develop improved methods of application or discover better repellents.

One hope that never dies is that a lotion or ointment can be developed that will be cosmetically pleasant and leave a long-lasting deposit of repellent on the skin. Many hundreds of formulations have been tested, and although some (e.g., lotions containing 40% of repellent and 5% to 10% of zinc oxide) were about as effective as full strength repellents, none were more effective. Likewise many efforts have been made, without notable success, to increase the retention of repellents in clothing through the use of various additives and processes. These lines of investigation are reactivated at intervals, however, and no one can say that they may not someday bear fruit.

Although many thousands of compounds have been evaluated as repellents, the search for better materials continues. The benzamides are still under investigation, as are the caprolactams, and tetrahydroquinolines. The tetrahydroquinolines appear to hold particular promise as clothing treatments foı ticks, fleas, and chiggers. However, these share most of the undesirable physical properties of the repellents now in use.

A great research effort is being made at the present time to determine the precise mode of action of the repellents. A clearer understanding of the way repellents produce their effects may point the way to completely new groups of compounds or methods of use.

Another goal which has long been sought is the repellent pill, or oral systemic repellent. In past years many of the conventional repellents have been administered to various laboratory animals, orally or by intravenous injection, without much effect on the susceptibility of the host to mosquito bites. Recently the whole field of systemic repellency has been approached by a number of research agencies with renewed energy. Much of the current effort is devoted to studies on the mechanism by which bloodsucking insects find their hosts, with the eventual purpose of developing ways to interfere with such mechanisms.

The repellents that are recommended for personal protection are of little use for application to animals. Because such heavy dosages are required, and the repellents are lost from the skin so rapidly, it is not practical to keep livestock treated with dosages of these materials adequate to afford continuous protection.

The material that is most widely recommended foı protection of animals is synergized pyrethrins. This is often supplemented in commeıcial formulations with such materials as 2,3,4,5-bis(2-butylene)tetrahydrofurfurol, dipropyl pyridine-2,5-dicarboxylate, butoxy polypropylene glycol, and dibutyl succinate.

It has been suggested that repellents could be used to advantage to treat cockroach harborages, especially soft drink cartons, cases, or boxes that might serve to transport cockroaches from infested to previously uninfested areas. A number of effective cockroach repellents have been reported to provide complete repellency for periods of several days or weeks. Among the best are 2,3,4,5-bis(2-butylene)tetrahydrofurfurol alone and with *N*-octyl bicycloheptene dicarboximide, *tert*-butylsulfinyl dimethyl dithiocarbamate, 2-hydroxyethyl octyl sulfide, and octyl propyl sulfoxide.

Much attention has been given to the development of repellents for insects affecting stored products. Such materials would be highly useful for the protection of packaged foods from insect penetration. Hundreds of the more effective mosquito repellents have been tested for this purpose, but none showed any practical advantage over synergized pyrethrins, which is the only material currently recommended. A few compounds of other types have shown promise in laboratory tests, but have not been cleared toxicologically for such use.

I know of no current recommendation for the use of repellents to protect plants from injurious arthropods. The few attempts to use mosquito repellents for this purpose have not

been successful. Much study has been given to the attractive and repellent material in the plants themselves, and the discoveries in this field may eventually lead to the development of repellents of practical value.

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BRACON VENOM—A NATURALLY OCCURRING SELECTIVE INSECTICIDE

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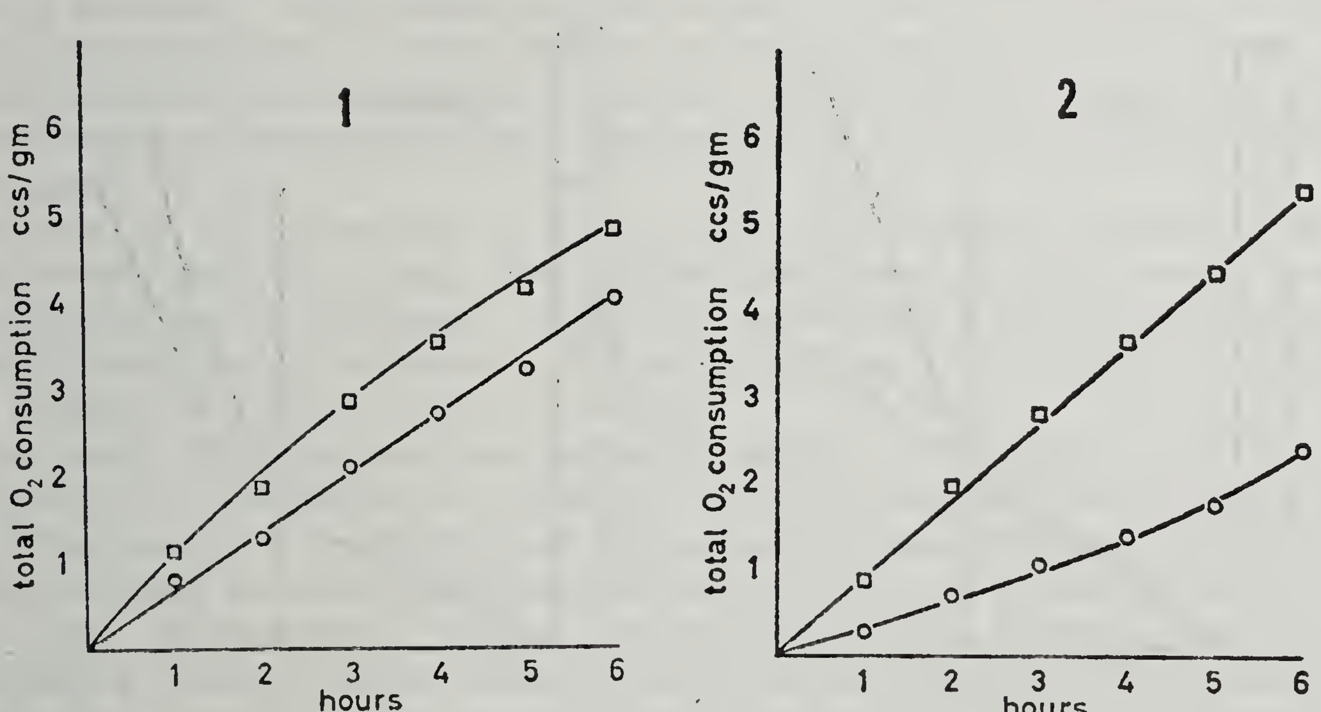
In view of the now well recognized need for insecticides more selective than the conventional ones (3), a study of some natural insecticides of arthropod origin has been undertaken. The venom from the parasitic wasp *Bracon hebetor* was chosen in view of its specificity and the ease with which the insect itself can be reared.

This wasp has a recorded host list of 25 species all of which are Lepidoptera. In addition it has been reared in this Laboratory on four other species of Lepidoptera. Injection of solutions of the venom in saline into a range of animals also showed that Lepidoptera are the only susceptible hosts.

Experiments in which venom solutions of various strengths were injected into larvae of the wax moth (*Galleria mellonella*) showed that the venom is extremely potent—5 μl of a solution containing 1 part of venom in 6×10^6 parts of solvent causing permanent paralysis.

The effect of the venom on the respiration of *Galleria* larvae was studied using the electrolytic respirometer described by Winteringham (4). *Galleria* larvae were weighed and injected with 5 μl. of venom solution and their respiration measured over a period of 6 hours. Control larvae were injected with 5 μl. saline. Fig. 1 shows that the respiration is reduced by the venom to about 80% of the control level. In view of the extreme flaccidity and complete paralysis of the larva this seemed a rather small reduction—however the results of several experiments were consistent. It was thought that there might be a difference between the venom as injected by the wasp and the venom solution made by extracting the glands with saline. So a group of *Galleria* larvae were exposed to some adult *Bracon hebetor*. The paralysed



Figs. 1 and 2. Oxygen consumption of *Galleria* larvae (1) paralysed by injection of a solution of *Bracon* venom, (2) paralysed by *Bracon hebetor*. Upper curves, control; lower curves paralysed larvae.

insects were then placed in the respirometer and their oxygen consumption measured over a period of 6 hours. In this case the oxygen consumption is reduced to about 40% of the control level (Fig. 2). Thus there is a difference in oxygen consumption between larvae paralysed by injection of the venom solution and those paralysed by the wasp. One explanation of this difference is that the venom as injected by the wasp probably comprises several components—this is in keeping with our knowledge of other insect venoms. One of these components then is responsible for the paralysing effect—probably acting as a neuromuscular blocking agent (1)—another acting as a respiratory inhibitor. Alternatively the larvae when exposed to the adult wasps may have been stung several times thereby receiving a larger dose than those injected with the venom solution.

Beard (1), using electrophysiological techniques showed that the most probable site of action of the venom was at the neuromuscular junction. Assuming this to be correct we have a valuable tool with which to study the mode of action of insecticides.

It is well known that DDT causes a large increase in the amount of oxygen consumed by an insect poisoned with this substance (5). This is usually attributed to the increased neuromuscular activity e.g., flight convulsions and tremors. However there is evidence that DDT affects oxidative metabolism *in vitro* in a more direct manner (6).

If a venom paralysed moth is treated with DDT no increase in oxygen consumption is observed (Fig. 3). This shows that the venom reduces the oxygen consumption of the DDT-poisoned insect. Furthermore a venom paralysed moth treated with DDT shows no signs of neuromuscular activity.

A large increase in oxygen consumption can be observed in insects poisoned with Dinoseb (2-*sec*-butyl-4:6-dinitrophenol) (2). This substance is an uncoupling agent i.e., the process of phosphorylation is uncoupled from the oxidation and the respiration of a poisoned animal would be expected to increase beyond that required for normal muscular activity. The effect of treating control and venom paralysed *Galleria* adults with Dinoseb is shown in Fig. 3. Although the moth treated with venom is completely paralysed it can be seen that the oxygen consumption rises steeply after treatment with Dinoseb.

Thus we have an insect whose respiration has been stimulated by two different methods. In the first instance DDT stimulates respiration by increasing neuromuscular activity. In the second instance Dinoseb stimulates respiration at the subcellular level by uncoupling the process of phosphorylation from that of oxidation. If the results of DDT and of Dinoseb treatment of *Galleria* adults are compared (Fig. 3) it is obvious that DDT has no uncoupling action *in vivo* since this insecticide does not alter the rate of respiration of the venom paralysed insect. It would also appear from these results that neither the respiration of the adult moth, nor the ability of an uncoupling agent to stimulate respiration is affected by the venom.

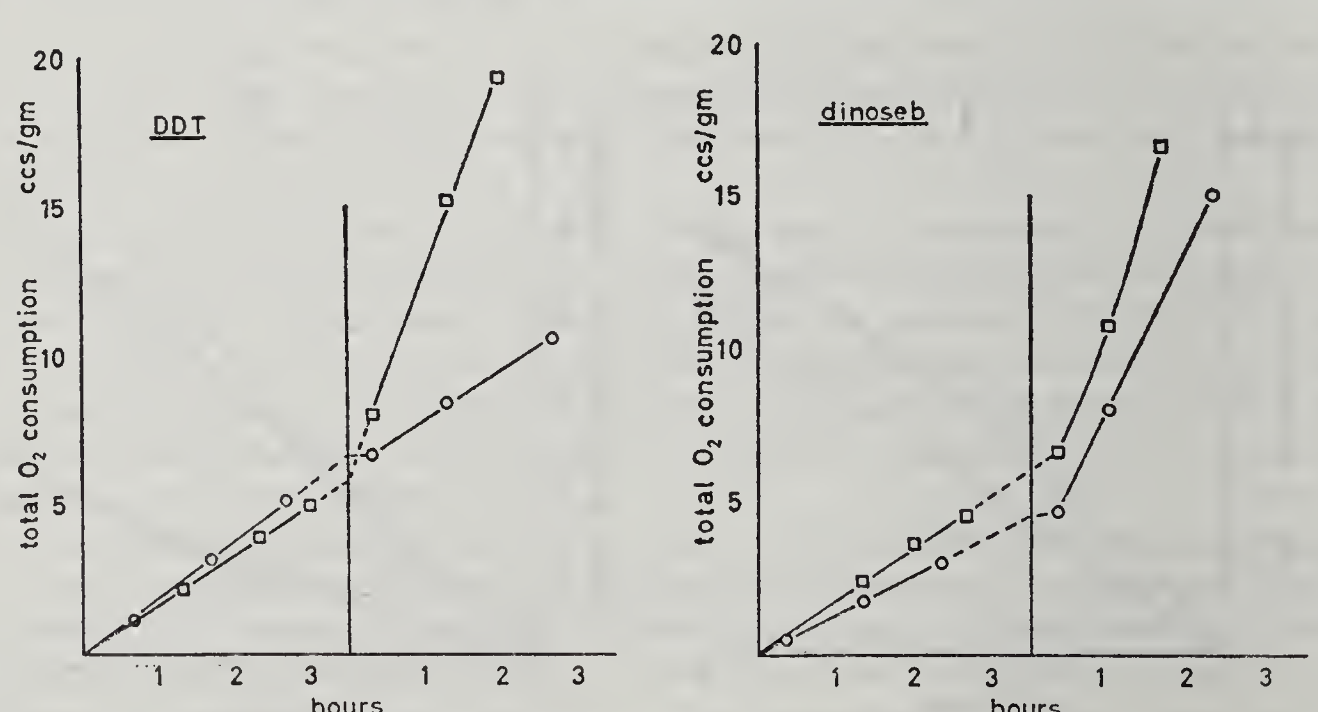


FIG. 3. The effect of DDT and of Dinoseb on the oxygen consumption of venom paralysed *Galleria* adults. Vertical line indicates time of treatment with insecticide. ☐ Control O Paralysed.

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INSECT CONTROL—WHERE NOW? (CHEMOSTERILANT SESSION)

THE PHYSIOLOGY AND TOXICOLOGY OF CHEMOSTERILANTS

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In general, research on chemosterilants has concerned itself with two types of materials: the antimetabolites and the alkylating agents. The former may be defined as a structural analog of a metabolite which competes *in vivo* for incorporation in an enzyme system to form an analog of a more complex, naturally occurring molecule. The latter is usually defined as a compound that can effect the addition of an alkyl group or compound radical with or without the replacement of a hydrogen atom in a biologically significant functional group under physiological conditions.

The first successes with sterilizing insects chemically were through the use of antimetabolites. Goldsmith and Frank (3) sterilized *Drosophila melanogaster* by incorporating the folic acid analog, aminopterin, (N-(p-([2,4-diamino-6 pteridyl) methyl] amino) benzoyl glutamic acid), in the adult diet, as did Mitlin et al. (11) with the house fly, *Musca domestica* L. This material, as well as other antimetabolites, caused sterilization of the female insect but was ineffective in the male. This differential effect appears to be the most serious disadvantage in the use of antimetabolites. In most insects of economic importance, sexual maturity in the male is attained before eclosion; hence the necessity of administering these materials in the diet, which can only be done after eclosion, and usually but not always precludes the sterilization of the male.

Tests were run with house flies to determine whether administration during the larval period might cause sterility (12, 9). The antimetabolites were found to cause a general inhibition of growth and development. They were not selective. The larval period was extended and pupation, when it occurred, was delayed. Flies that did pupate were generally abnormal in shape, and did not survive to eclosion.

In the adults, the antimetabolites are more selective. Generally, in holometabolous insects, growth of the tissues has been attained at eclosion, except for the ovaries, which are infantile. The metabolic activity of these organs makes them a primary target for the antimetabolites, resulting in a selective uptake of the chemical and a consequent inhibition of growth (11, 18). King and Sang (6) in an exhaustive study of the *Drosophila* ovary, concluded that aminopterin poisoned ovarial chambers that were actively synthesizing yolk, but had little effect on chambers in earlier stages. They noted that many of the completed oocytes were abnormal, and if laid, were non-viable. They reported that recovery from aminopterin-poisoning took place but some females failed to lay eggs because of blockage of the oviducts by abnormal eggs.

In the parasitoid wasp, *Bracon melitor*, an insect which has mature ovaries at eclosion, another folic acid analog, methotrexate (N-[p-{2,4-diamino-6 pteridinyl) methyl] methylamino} benzoyl] glutamic acid), caused atrophy of nurse cells and degeneration of the oocytes (4). Poor egg production was traced to difficulties in mitosis and differentiation.

While there is little specific evidence for the mode of action of the antimetabolites in insects, from work with other organisms it is believed that these materials interfere with the C_1 transport in biochemical conversion. In some microorganisms both aminopterin and methotrexate form enzyme complexes displacing particular derivatives of folic acid from the normal enzyme sites. Aminopterin has been shown (16) to have 1,000 to 10,000 the affinity for folic acid reductase as folic acid. Since the available evidence indicates that the reduced form of folic acid is the active form, it is apparent why growth is inhibited. It has been shown in liver preparations that the formyl derivatives of reduced folic acid are directly involved in purine metabolism, probably transferring a C_1 unit at the oxidation level of a hydroxymethyl group.

This ability to disturb nucleic acid metabolism in some fashion has formed the basis of considerable research on growth inhibition, particularly among those studying neoplastic tissues. Many unnatural analogs of nucleic acid bases have been synthesized and tested for their growth-inhibitory properties. When tested on house flies, several of them have been found to inhibit gonadal growth (10). In the boll weevil (*Anthonomus grandis* Boh.), as a consequence of finding significant amounts of guanine in the feces, (13) several guanine analogs were tested and two, 8-bromo guanine and 9 methyl, 2 butyl guanine have been found to be effective ovarian growth inhibitors. The testing of the guanine analogs was predicated on a hypothesis, not yet proven, that there was a low titer of the enzyme guanase and since at least one guanine analog, 8-azaguanine, is essentially detoxified by this enzyme in other organisms, possibly this as well as other analogs might prove to be effective. 8-azaguanine was not effective in this instance.

Greatest success in chemosterility has been achieved using the alkylating agents, chiefly because male sterility can more readily be attained. Two of the more effective compounds have been apholate (2, 2,4,4,6,6-hexahydro-2,2,4,4,6,6-hexakis(1-aziridinyl)-1,3,5,2,4,6-triazatriphosphorine), and TEPA (tris(1-aziridinyl phosphine oxide)). Several cytological studies of the effects of apholate on the gonads have been made. Morgan and LaBrecque (14) noted that the greatest effect of the chemical on the housefly was on the nurse cells of the ovary 72 hours after eclosion.

Chromatin was clumped in irregular masses and the nuclei had bizarre shapes. Although the oocytes in the first egg chamber matured, all of the cells in the second chambers remained undeveloped. Murray (15) noted similar effects in the mosquito, *Culex pipiens quinquefasciatus*. He found no or vestigial germaria in the ovary. In blood-fed females there was a reduced number of primary and often no secondary follicles. In the male, testicular growth was retarded, vacuolization occurred, immature sex cells were absent and there were few mature sperm. These effects varied with the dosage level.

There has been little reported about the metabolism of the alkylating agents in insects. P^{32} labelled methaphoxide, (tris(2 methyl-l-aziridinyl)phosphine oxide) was administered to the larvae and adults of the mosquito *Culex tarsalis*, and to houseflies (17). The flies were found to degrade 50% of the dosage within 2 hours. When the excretory products were examined, methaphoxide and a single breakdown product, presumably phosphoric acid, were characterized by paper chromatography.

Despite some inconsistencies, the general consensus of those who have studied the alkylating agents is that the nucleic acids, particularly DNA, are vitally affected. Chromosome breakage takes place only during interphase in plants (1), when they are treated with the nitrogen mustards. This implies some effect on DNA synthesis which occurs at this time. However, in *Drosophila*, mustard gas acts on sperm stored in the spermatheca of the female, presumably when no DNA synthesis takes place.

Nevertheless, study of structural requirements for cytotoxic action shows that cytotoxicity ran parallel to chemical activity (5). In addition, difunctional agents acted at lower doses

than monofunctional agents. This suggested that the linkage of large fibrous molecules like DNA involved in cell division might account for the higher toxicity of the difunctional agents. Also, the mutagenicity of these materials points directly to the genetic material being involved.

The most significant evidence on this question comes from studies of effects of alkylating agents on DNA-containing viruses (7). Other studies (8) have shown that DNA viruses are the most readily inactivated of all biological systems examined. It appears that the number 7 position of the guanine moiety is most susceptible to alkylation.

Opinions differ on how an alkylating agent affects the DNA. Many workers favor the cross-linking theory. This holds that the alkylating agent causes a linking between or within each strand of DNA (2). However, other workers favor the concept that enzymes are deactivated by reaction of the alkylating agent into a functional group of the enzyme. Still others feel that an antimetabolite is formed which inhibits enzyme synthesis (19). At the moment there is no final answer.

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CHEMOSTERILANT TREATMENT OF TWO GREENHOUSE SPIDER MITES

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Untreated females of *Tetranychus telarius* (L.) mated with males dipped in 0·5% apholate in alcohol-water solution, produced male progeny and dead eggs but no female progeny. Females exposed to 2% apholate dip produced no viable eggs and assumed the distinctive translucency of body content and disappearance of two dark pigmented spots typical of apholate sterilization. When supplied 10 virgin females, apholate-treated and normal males mated with an average of 3·6 and 6·4 females, respectively.

Adult females, allowed to feed on plant foliage previously dipped in 1% aqueous apholate, ceased egg-laying after a few days and became sterile. Most adult males fed for 24 hours on apholate treated foliage were sterilized. When compared with untreated females, females allowed to feed on residues then mated with normal males, laid fewer eggs that produced fewer male and fewer female progeny as well as numerous dead eggs. Some female progeny of treated females but not of treated males developed apholate-sterile characters even though reared from eggs laid on untreated foliage. Apholate residues on foliage persisted for at least 4 days.

In tests to determine prevention of population build-up, 3 resistant strains and 1 nonresistant strain of *T. telarius* and the nonresistant *T. cinnabarinus* were allowed to feed on treated plants. Susceptibility of *T. cinnabarinus* and the 4 strains of *telarius* to apholate varied only slightly.

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OVIPOSITION-INHIBITING AGENTS: A SCREENING FOR SIMPLE MODEL SUBSTANCES

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During the last three years the main emphasis in the chemosterilant field has been laid on aziridine derivatives. However, these substances are hazardous to mammals. One should search for compounds that would be safe, even if applied in the same way as insecticides nowadays.

In a screening, we treated female houseflies with numerous solvents by topical application (three-day-old females from mixed populations, kept on water and sugar). They were then placed with the same number of males into containers. The treated females were offered milk and cube sugar for 48 hours, after which time the milk was withdrawn and a black oviposition pad wetted with water offered. The containers were inspected once a day for oviposition and adult mortality. Eggs were counted singly.

Low dosages of topically applied benzene apparently stimulate egg-laying. At higher dosages, benzene reduces egg-laying. Oviposition is also reduced by cumene, by tetrahydrofuran, by anisol, by furfural and by bromobenzene.

Most experiments were carried on for 14 days after the withdrawal of milk and were interrupted thereupon. Later on, some of the solvents found to be active were retested in complete life-cycle experiments.

Replications in life-long series seemed to confirm the activity of benzene, bromobenzene, tetrahydrofuran and furfural. Female housefly fertility can thus be affected by very simple substances.

Another simple compound, *m*-xylohydroquinone, prevents oviposition when fed at a rate of 0·1% in the females' and males' food (1). Feeding 0·1% of *m*-xylohydroquinone to males for 3 days had no appreciable effect on the fertility of eggs from females mated to the treated males. However, at 0·15% and 0·2% there was a strong sterilizing effect on males when they were fed on the compound for the first three to five days of their adult life.

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THE CHEMISTRY AND PROPERTIES OF INSECT CHEMOSTERILANTS

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Historically there is a connection between the development of cancer therapeutic agents and insect chemosterilants. The cancerous cell is in many respects similar to embryonic cells (sperm, ovum) and the ultimate aim, i.e. the interference with cellular reproduction, was the same for cancer chemotherapy and insect sterilization. Indeed the first compounds which acted as chemosterilants were antitumor agents or at least compounds closely related to them.

Chemosterilants can be divided into three categories: antimetabolites, biological alkylating agents, and miscellaneous compounds. The first two groups are well known in cancer research and it was the last group where a radical departure from the cancer-sterilization relationship was indicated.

Our recent work uncovered a structurally related series of compounds which can be loosely designated as amides. We have described two of these compounds hexamethylphosphoramide (hempa) and hexamethylmelamine (hemel) in a recent publication (S. C. Chang, P. H. Terry, and A. B. Bořkovec) and have, in the meantime, extended the research to other related compounds.

Although the active amides are often strikingly similar to active aziridinyl compounds (compare hempa with tepa) there are many important differences between their chemical and physiological properties. One of the main obstacles in the development of practical insect control methods based on chemosterilants was the toxicological aspect of the most potent chemosterilants, the aziridines. Tepa, metepa, apholate, and tretamine are all mutagenic agents in bacteria, the last compound being one of the strongest mutagens known. Although mutagenic activity in bacteria (*Escherichia coli*) does not necessarily indicate similar activity in mammals, mutagenic or carcinogenic compounds must be handled with extreme caution and their application restricted to uses where human or other animal exposure is minimized or entirely avoided. The two amides, hempa and hemel, are not known to possess mutagenic activity and their physiological activity in higher animals is entirely different from that of the aziridines. These differences are not surprising in view of the fact that the aziridines are biological alkylating agents whereas the amides are devoid of alkylating properties. There is one additional advantage which makes the amides attractive as chemosterilants. The aziridines are rather reactive compounds which decompose or polymerize to nonsterilizing products when exposed to acids, bases, or increased temperatures. This characteristic imposes another restriction on their use and formulation. The amides, on the other hand, are usually quite stable and their residual activity is expected to surpass that of the aziridines.

From a more academic point of view, the chief contribution of the discovery of activity of the amides lies in the realization that insect chemosterilants need not be only compounds which are highly physiologically active toward all living organisms. The ideal control agent is a highly selective one and the new chemosterilants indicate that such an ideal can be reached or at least approached even in the insect sterilization control method.

CHEMOSTERILANTS FOR THE CONTROL OF INSECTS

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Chemosterilization is an extension and amplification of the sterile male technique, the principle of which was so vividly proven in the screw-worm, *Cochliomyia hominivorax* (Cqrl.), eradication programs. This fascinating concept is still in its infancy, but if directed properly it has great potential in the control and eradication of ecologically and geographically delineated insect populations.

Chemosterilants might be used in two ways. They may replace the irradiation method for sterilizing large numbers of insects at a permanent site or methods may be developed by which they can be used in the field by incorporation in the food of adult insect populations, application to the breeding medium, residual applications in selected resting areas, or inclusion with an attractant in a bait. The use of sterilants to sterilize insect populations would preclude the necessity of rearing and releasing astronomical numbers of insects.

Investigators at the U.S. Department of Agriculture laboratory in Orlando, Florida (now located in Gainesville, Florida) have found some 112 chemicals that possess sterilant activity, the majority of which are antimetabolites and alkylating agents. Although the biological effects of alkylating agents are more severe than those of the antimetabolites a number of promising sterilants have been found in this group, and tepa (tris(1-aziridinyl)phosphine oxide), metepa (tris(2-methyl-1-aziridinyl)phosphine oxide), and apholate (2,2,4,4,6,6-hexakis(1-aziridinyl)-2,2,4,4,6,6-hexahydro-1,3,5,2,4,6-triazatriphosphorine) have been utilized successfully in laboratory and field experiments.

Recent laboratory studies have shown several dimethylamine derivatives to be effective sterilants. The structure of these chemicals closely resembles that of some of the more promising alkylating agents, but these materials apparently do not possess all the radiomimetic activity of alkylating agents. Promising representatives of this group are hemel (hexamethylmelamine) and hempa (hexamethylphosphoramide).

Chemosterilants are receiving increased attention as a promising approach to control and to date, more than 25 species of insects have been sterilized in the laboratory in various areas of the world. In small controlled field experiments, house fly, boll weevil and Mexican

fruit fly populations have been significantly reduced or eliminated by means of chemosterilant baits or releases of chemosterilized insects.

Studies on insect behavior, sterilant dosages, mating competitiveness and mode of sterilant application for each species must all be resolved prior to the initiation of field trials. Many investigators have already completed these preliminary phases with certain species and should soon initiate field studies. Although recommendations for the practical use of chemosterilants cannot be made at the present time, their potential usefulness in control of some species has been demonstrated with the materials now at hand. The full potential of this method of control will depend on the results of toxicological investigations now in progress with the chemosterilants now available and the development of superioı materials.

THE EFFECT OF CHEMOSTERILANTS ON THE DEVELOPMENT OF REPRODUCTIVE ORGANS IN INSECTS

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In the Entomological Institute of the Czechoslovak Academy of Sciences the development of insect reproductive organs has been studied for several years. In this investigation during the last two years we have studied the effect of some cytostatics on the development of reproductive organs, especially on the ovaries of the house fly, *Musca domestica*. For this experiment a standard strain S.R.S. (*Musca* I) from Italy was used. These flies were kept in silon cages at a temperature of 25°C and a humidity of 60%. The adults received the substances dissolved in water. Twenty cytostatics used in Czechoslovakia were tested for their chemosterilizing effect. Chemosterilizing effect was shown by the following substances: 6-azacytidine, 5-azauracil, 6-azauracil, demecolcin, dibromaminopterin, endoxan, carbimazol, difostilben, mercaptopurin, TS 160, thyminalkylamin.

The investigation was done from the point of view of anatomy and histology. The development of ovarioles affected by 6-azauracil riboside, aminopterin and thiotepa was studied in detail. For this study the anoptral contrast and histological methods were used. The material was fixed by Carnoy's fluid and stained by the Masson's trichrome stain with Heidenhain's hematoxylin.

The normal development of ovaries goes through 5 phases. In the first phase the egg chamber remains as a part of germarium. In the second phase the egg chamber is distinctly separated. In the third phase the nurse cells form the yolk which quickly grows and fills up the oocyte. In the fourth phase, the membranes of the nurse cells disappear and their nuclei show the beginning of pycnosis. In this phase the chorion formation also begins. The egg is laid and the empty follicle purse remains and the corpus luteum disappears after a very short time. The whole development takes approximately 10 days.

The second egg chamber separates from the germarium about the second day of development. The third and the fourth phases of development of the second egg chamber proceed faster than the first one. The third egg chamber appears at the beginning of the growth of the second egg chamber and sometimes even earlier.

Comparison of the effect of chemosterilants on the development of ovaries of the house fly can be demonstrated by the effect of gamma-rays. House flies in the pupal stage just before emergence were irradiated by a dose of 3000 and 4000 rad/5 min. The evident changes proceed from the germarium to the first egg chamber. At the beginning of the third day the germarium degenerates. The degeneration of the second egg chamber follows. The first egg chamber develops at first and reaches the end of the third phase in which the yolk is formed. The nurse cells degenerate in this phase at the same time and the progressive degeneration and the resorption of the first egg chamber takes place. Follicle cells show an evident degeneration consisting of pycnosis etc. The rapid proliferation of cells did not take place in the cases studied.

After application of 6-azauracil riboside the development is gradual and quite regular up to the beginning of the third phase of development of the egg chamber. In this time the nuclei of the follicle cells begin to grow. Their basophility increases and doubled nuclei

appear in all follicle cells. A rapid growth of follicle cells follows in several days. The multilayered follicle epithelium is formed. The cells migrate inside the egg chamber which is ful of yolk and the nurse cells form a rough surface. The cells are variable and abnormal. They have nuclei of a different size with evident phases of division. Many of them are amitotic. At the beginning phase of the proliferation of follicle cells the nuclei are active. After that their pycnotic cells degenerate. This is evidently an example of rapid tumorous growth. Nurse cells develop regularly even the rapid proliferation of follicle cells begins. Later great chromatin clusters appear in the nuclei and their secretion activity is abnormally great.

After the phase of the proliferation a phase of rapid degeneration of the tumour takes place with a following resorption both the degenerated cells and the remaining contents of the egg chamber. The whole egg chamber becomes smaller and the vitelline membrane formsl folds which in the final phase fill up its whole lumen. The second oocyte remains all this time in the second phase and there are no changes on its surface. During the application of 6-azauracil riboside there are no evident changes of the germarium.

The application of aminopterin shows the same results as 6-azauracil riboside. Simultaneously with the rapid proliferation the hypertrophy, pycnosis and degeneration of nuclei of the nurse cells take place. The changes are of a more rapid character than in case of application of 6-azauracil riboside and they come much earlier. The degeneration of follicle tumour and the resorption are the same as with 6-azauracil riboside.

In contrast to 6-azauracil riboside, aminopterin even causes changes of the second egg chamber. The changes are not of tumorous character. In the final phase even the germarium degenerates.

After application of thiotepa the rapid proliferation is immediately followed by a degeneration. At the end of degeneration the cells completely disappear and the egg chamber is full of an amorphous mass with large basophil clusters. The egg chamber loses its regular form, it is several times constricted and eventually it takes different anomalous forms.

To compare with the influence of cytostatics the effect of thalidomide was also studied. After the application of thalidomide the growth is interrupted before the formation of the yolk or in its early phase. The egg chamber remains in this stage all during development. At the end of development the membranes between the cells of the follicular epithelium completely disappear. In the zone of follicular epithelium small pycnotic nuclei remain situated somewhat to the centre of the lumen. From the nurse cells remain only the pycnotic nuclei.

From the above mentioned results it is evident that there is a specific way in which the chemosterilants effect ovariole development. It consists in the formation of tumorous cells and in their following degeneration. Thus it is evident that the effect of chemosterilants differs from the effect of gamma rays and other chemical materials.

TRIPHENYL TIN COMPOUNDS AS INSECT REPRODUCTION INHIBITORS

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Using the house fly as an indicator, a number of triphenyl tin derivatives were found to act as reproduction inhibitors. The more active compounds such as Dowco* 186 (triphenyl tin hydroxide), Dowco 187 (allyl triphenyl tin) and Dowco 188 (bis triphenyl tin) sulfide) have three phenyl groups in common, plus a fairly labile fourth group attached to tin. The above compounds sterilize adult flies well below the lethal concentration. Females are sterilized at lower concentrations than males. Some derivatives produce easily reversible reproduction control; some do not. This property is somewhat dosage dependent in the house fly with all gradations ranging from nearly complete ovarian suppression to deposition of normal sized but sterile eggs. Triphenyl tins suppress or control reproduction in the German cockroach and the confused flour beetle. The triphenyl tin moiety would appear to have promise for the reproduction control of insects and related species from a number of orders of arthropods.

*Trademark of The Dow Chemical Company

SECTION 9a.—AGRICULTURAL ENTOMOLOGY

The following paper was read but the author did not wish it to be published here:

Wallace, M. M. H. (Australia). The ecological basis for effective control of the lucerne flea (Collembola) and the red-legged earth mite (Acari) in Western Australian pastures.

EPIDEMIOLOGY AND CONTROL OF INSECT-BORNE PLANT VIRUSES

ENVIRONMENTAL CONDITIONS OF VIRUS TRANSMISSION—A BASIS FOR DISCUSSION

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The transmission of virus diseases in field plots and in horticultural districts shows a complicated relation between vectors, their food plants, diseased plants and plants grown for food or as ornamentals. This relation becomes even more complicated because not only one

virus belongs to the cycle of vector, infection source and cultivated plant, but a group of different viruses of the non-persistent and persistent types is involved in virus spread in general. Whereas each persistent virus has a limited number of vectors, a non-persistent virus may have 30, 50, or even more vectors. However, the number of persistent viruses of economic importance is not large.

In Germany and Western Europe one of the most destructive viruses is potato leaf-roll virus; this and other important ones are all aphid-transmitted viruses. Some leafhopper-transmitted viruses are of minor importance, such as green petal of strawberry and European leafhopper-borne clover stunt. One, transmitted by beet-bugs (*Piesmidae*), is an important disease on sugar beets in Central Europe; another, transmitted by thrips, is more or less a disease in temperate or warm climates. Of the persistent viruses, the aphid-transmitted and the beet-bug-transmitted viruses seem to have the most important effects on crop-losses. The semi-persistent type is represented by one of the most destructive viruses, aphid transmitted sugar beet yellows, on sugar beet in western Europe.

Most of the viruses causing diseases occurring in Western Europe are non-persistent. Because of the short time needed for their uptake and inoculation, it is not difficult for an aphid to act as a vector, even only occasionally. Thus there are large numbers of vectors, with an enormous and rapid spread, for this type of virus, if the conditions are favourable.

The way the aphid hibernates strongly affects virus spread. In a moderate climate large numbers of aphids (e.g. the green peach aphid) overwinter as the viviparous summer form. Virus transmission then starts very early in the year, when suitable plants are available. Inspection in different countries has shown that aphid infestations in the neighbourhood may originate from greenhouses. Storage rooms for potatoes, for vegetables and beet clamps are also possible hibernation places and aphids remain active there when the temperature reaches more than 5°C. Thus virus transmission goes on in beet clamps or in storage rooms with sprouted potatoes and they may even become infected to a significant degree before planting.

The change in hibernation sources by growing new varieties or new species of perennials, or shrubs or trees, may profoundly alter the possibilities for hibernation. Partly the influence extends to the virus which can overwinter in suitable perennials in urban or suburban districts, partly the vector is favoured by host plants, which are new to an area.

The greater the distance between the winter-host plants and the seed-potato fields, the smaller the number of arriving aphids, and the later colonization of the potato plants. Potato plants in an early stage of development are very susceptible to virus infections and for this reason the later the arrival of winged vectors the better for potato growers. The main time for the spread of viruses is during the summer flights, which begin earlier in districts with numerous winter hosts. Early flights are announced to the seed producing areas so that spraying, haulm killing, early roguing or other suitable measures may be taken. In other crops a number of other environmental conditions may influence the virus transmission during the vegetative period. On fields with alfalfa, clover, peas or other legumes one of the main vectors, the pea aphid, develops on the field crop during the whole year; there are no great losses caused by migration from winter host plants but spring weather conditions are important.

Favourable spring weather makes it possible for an early mass-production of aphids, an early overcrowding of young plants and the development of many winged aphids with all the consequences of an early virus spread. Cutting of alfalfa or other forage crops at times of large aphid infestations contributes to an extended aphid movement; the number of aphids diminishes rapidly but within a short time the young fast-growing shoots support masses of aphids. Predators are relatively few on these young shoots for many are removed by the cutting.

A similar effect may occur with weed control, when the plants have grown enough to be colonized by aphids. A chemical weed control kills the older plants so slowly that aphids have a chance to change to cultivated plants. Some aphids drop down immediately in big numbers when the host plant is touched. Afterwards some walk away to new plants, probe and walk about till they have found a suitable host. In this way they also spread virus. Early weed-killing before germination of the cultivated plant ensures that the weeds do not serve as hosts for aphids. Weeds with tap-roots, stolons or deep rooting weeds offer special conditions in spring; it is hard to destroy them with normal weed-killers. They may already

contain virus from the preceding year. Special control measures in late spring or early in the summer are necessary to kill these plants. Yellow colour is very attractive to winged aphids and fields with yellow-flowered weeds may attract big numbers when the flowering coincides with periods of flight which may influence virus spread.

The whole complex of aphid vectors, host plants of aphids, viruses, infection sources, weeds and perennial ornamentals as host plants for both virus and vector is a very complicated system which is illustrated diagrammatically in fig. 1:

Beginning at the left, aphids go from the winter to summer host, or from a greenhouse or a perennial weed. These are only the main possibilities of migration. It is certain that aphids from winter hosts are virus-free (in greenhouses gardeners remove diseased plants as early as possible). It is suggested that the aphids coming from greenhouses or from the winter hosts, at first visit a perennial virus-infected weed or cultivated plant. If the aphid is polyphagous it may fly to a perennial or to a weed and many transmit the virus to the first plant it visits. The progeny which developed on the perennial also becomes infectious and may visit new host plants and infect them. From weed No. 1 the polyphagous vector may distribute the virus to the neighbouring summer host plants. An oligophagous vector with a limited number of host plants spreads the virus to other hosts, also to weeds with monophagous vectors which feed and propagate only on that species of weed. This vector infects plants near the first infected plant of the group which it colonizes, and from these weeds an oligophagous or polyphagous vector takes up the virus and transmits it to perennials or perennial weeds. Therefore in addition to the transmission cycle of oligophagous or polyphagous vectors, a transmission cycle of monophagous vectors of minor importance may exist. During the summer, polyphagous, oligophagous and monophagous vectors provide for a general spread of viruses and the more plant species exist in an area, so more aphid species become involved in the complicated transmission cycle and more plants will become infected.

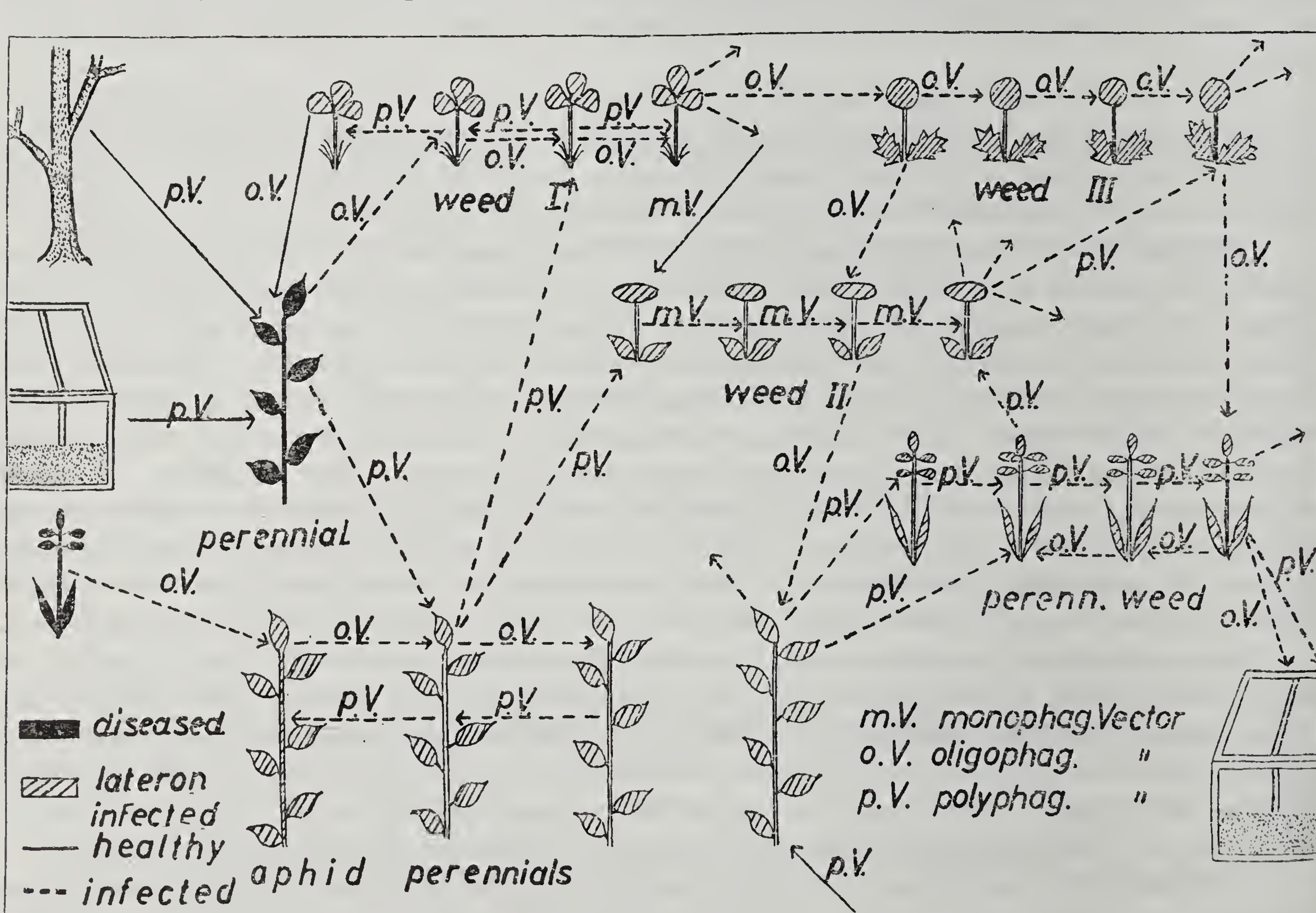

FIG. 1. Diagram of vector—host system.

TRANSMISSION OF SUGAR BEET VIRUSES IN RELATION TO THE FEEDING, PROBING AND FLIGHT ACTIVITY OF ALATE APHIDS

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The three commonest viruses affecting sugar beet in the U.K. are the non-persistent beet mosaic virus (BMV), the semi-persistent beet yellows virus (BYV) and the persistent beet mild yellowing virus (BMYV). The following considers some of the factors that may affect the long distance transmission of these viruses by the aphid vectors, *Myzus persicae* and *Aphis fabae.*

The time that alate aphids may act as virus vectors is normally restricted to the first few days of adult life, before their flight muscles autolyse (5), and there is circumstantial evidence that most aphids migrating long distances are on their first, or early, flight. This is indicated by the fact that the changes in numbers of aphids flying at different heights in the air also reflects changes in numbers flying from plants for the first time (7, 10). Thus long distance transmission of aphid-borne viruses probably depends partly on the ability of aphids that have developed on infected plants to carry viruses from those plants on their first flight.

Fig. 1 shows the results of experiments in which aphids were tested for infectivity after developing and flying from infected beet plants. 16% of *M. persicae* were infective with BMV, but no *A. fabae.* This difference is more associated with a difference in probing behaviour at the end of the flight-maturation period than with a difference in the intrinsic ability of the two species to transmit BMV, for under optimum conditions for acquisition of this virus, a 1 min. feed on infected plants, alatae of the two species are about equally efficient vectors (2).

With BYV, 27% of *M. persicae* were infective on flying from infected plants, but only 2% of *A. fabae.* This difference probably reflects a difference in the inherent ability of the two species to transmit BYV, for after the optimum time for acquisition of this virus, about 20 hours on infected plants (11), the difference in infectivity of alatae of the two species is about the same as that of alatae flying from infected plants for the first time (4).

Over 70% of *M. persicae* flying from BMYV-infected plants were infective, but no *A. fabae.* This supports conclusions (9) that *A. fabae* is either not a vector, or a very poor vector, of this virus.

These results show that *M. persicae* alatae are much more efficient than *A. fabae* at transmitting viruses from infected beet plants on which they have developed. Thus, although often less common in beet crops than *A. fabae*, *M. persicae* alatae are probably much more often responsible for carrying beet viruses over long distances. Also, the greater proportion of *M. persicae* alatae that are infective on flying from BMYV-infected plants than are infective

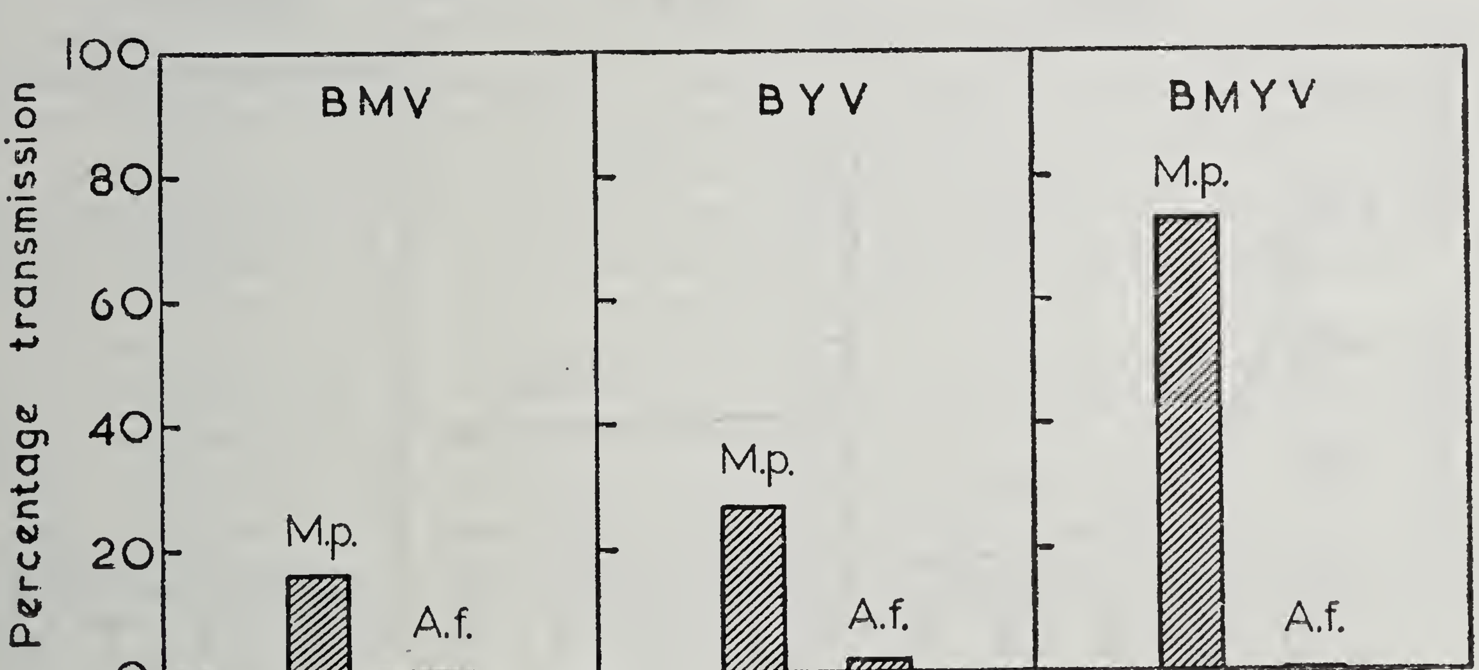

Fig. 1. Infectivity of alatae after developing and flying from sugar beet plants infected with beet viruses. Each result is based on the number of transmissions by 40-150 aphids tested singly, in pairs or in groups of three. From the number of test plants that became infective an estimate was made of the number of infective aphids using the conversion of Gibbs and Gower (1960).

on flying from BYV-infected plants, may be one of the reasons why BMYV is generally more widespread, and sometimes spreads more quickly, than BYV (9).

Probably one of the main factors affecting the distance that aphid-borne viruses are transmitted is the length of time aphids remain infective during flight. To study loss of infectivity during flight, aphids were flown while suspended with adhesive from pins in an air current corresponding approximately to their own flight speed (2). Fig. 2 shows the infectivity of alatae that had developed on infected plants and had then flown for up to 4 hours at 25°C.

There was a rapid decrease in the ability of *M. persicae* alatae to transmit BMV during the first hour of flight; this undoubtedly limits most transmissions of this virus to short flights (12). However, about 6% were still infective after flying for 4 hours, and this suggests that a few aphids may transmit this particular virus after long natural flights. During a flight of 4 hours duration, even in winds of moderate speed, an aphid could be carried 20-40 miles.

The usual temperature range for aphid flight is about 15-30°C (1, 6), and temperatures within this range affect the persistence of non-persistent viruses in aphid vectors, the viruses persisting longer at lower temperatures (2). Thus low air temperatures may increase the distance that such non-persistent viruses as BMV are carried.

Long distance transmission of non-persistent viruses, however, depends not only on the aphid remaining infective during flight, but also on the infective aphid alighting and feeding on a susceptible plant without first alighting and feeding, even briefly, on non-susceptible plants. Thus 10% of *M. persicae* alatae from infected plants transmitted BMV after they had flown for 1 hour and then fed immediately on beet plants; none transmitted after they had flown for 1 hour and then fed for 5 minutes on broad bean plants (not susceptible to BMV) before feeding on beet plants. The ease with which aphids can lose their infectivity by probing non-susceptible plants obviously greatly lessens the chances of their transmitting non-persistent viruses after they have flown long distances (8).

There was no significant decrease in the infectivity of alatae with BYV or BMYV during flights of up to 4 hours (fig. 2), and the results indicate that there would be little decrease even during more prolonged flights. These viruses could obviously be transmitted over much greater distances than the non-persistent BMV.

The infectivity of aphids with BYV decrease during the 3-5 days that most of them retain the ability to fly, whereas there is no significant decrease in the infectivity of aphids with BMYV during this time. Thus 22% of *M. persicae* alatae flying for the first time from BYV-infected plants were infective, but only 2% of these were infective 3 days later (4); by contrast,

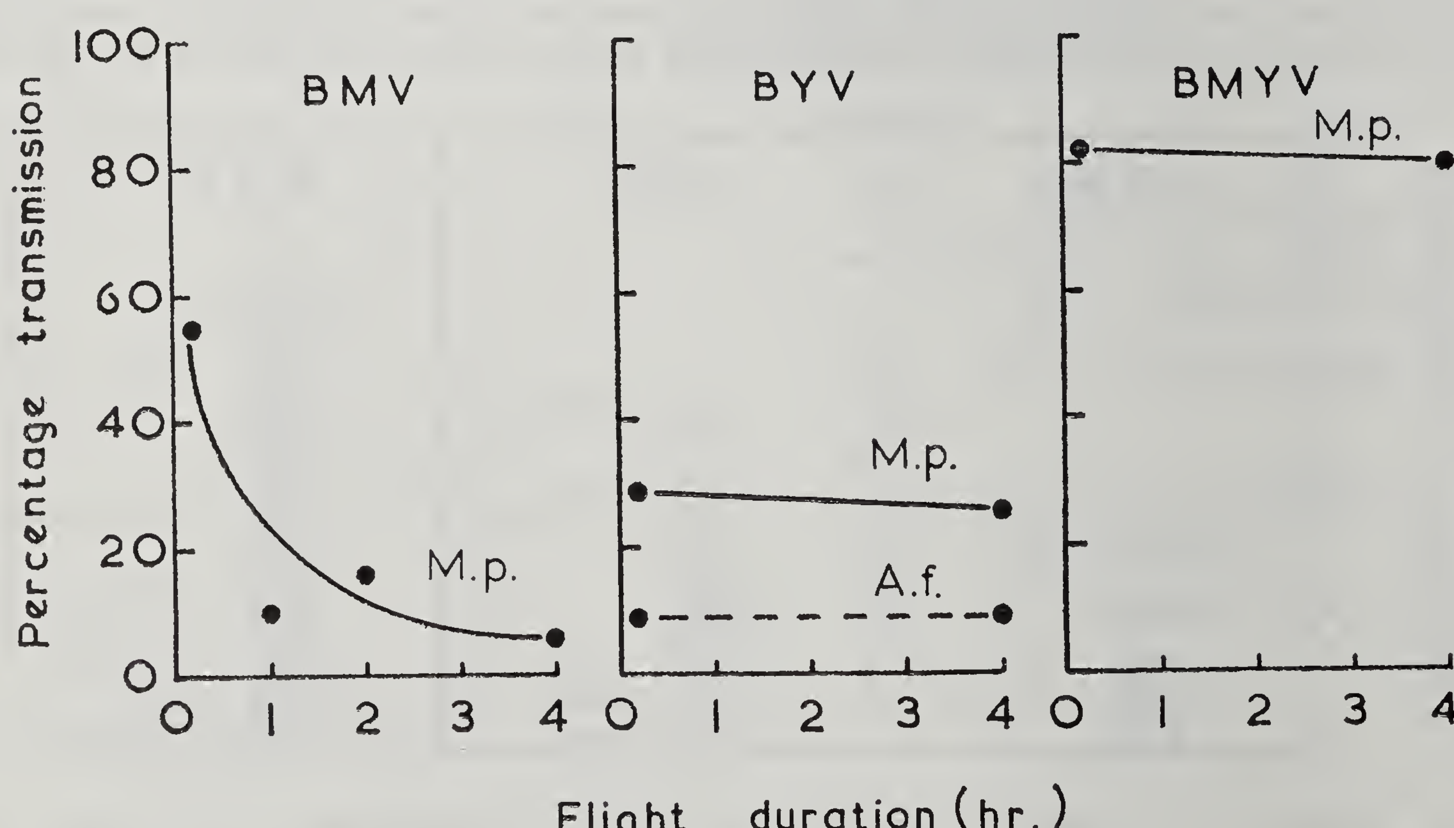

Fig. 2. Infectivity of alatae after flying for different times. Each point is based on the number of transmissions by 40-60 aphids tested singly, in pairs or in groups of three (see legend for fig. 1).

the corresponding results with BMYV were 75% infective alatae on the first day, and 72% on the third. The greater persistence of BMYV than of BYV in *M. persicae* is probably another reason why BMYV is more widespread, as already suggested by Russell (9).

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THE IMPORTANCE OF ALATE APHIDS IN VIRUS SPREAD WITHIN CROPS

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Winged aphids carry viruses from one crop to another, but do they play any significant part in spreading viruses within crops? The foci of infected plants that often occur around the original infectors led most people to assume that spread within the crop was mainly by wingless aphids, but those who have watched flying aphids noted that they flew from plant to plant, or over short distances of a few feet, or were swept away by the wind. It is difficult to determine whether viruses are being spread by walking or by flying aphids under field conditions, for apterae must be preceded by alatae, and it is impossible to have an apterous population present without risking visits from alatae, unless the work is done under large cages, and then alatae may develop from the apterous population.

Several experimental techniques have been devised to study aphid movement in relation to virus spread. In Sweden, aphids were caged on sugar beet plants infected with yellows virus and treated with radioactive phosphorus. About a week after the cages were removed most radioactive aphids were found within one metre of the point of release, and Björling, Lihnell and Ossiannilsson (1951) argued that as no radioactive alatae were found, the foci of infected plants that developed around the source plants were caused by apterae. However, most infected plants had no aphids on them, and it was impossible to distinguish the infections caused by the released aphids from those by the small natural population.

Broadbent and Tinsley (1951) used sticky boards surrounding potato plants to prevent aphids walking from adjacent infected plants; an equal number of unprotected plants could be visited by both walking and flying aphids. Results in three years indicated that 77-100% of the spread of virus Y and 87-100% of leaf roll virus was by alatae.

Experiments on the time of virus spread within potato crops have shown that alatae play a large part in the process. Initial colonizers come from other plants and are not carrying potato viruses, which they pick up from plants within the crop. Usually about half of the season's virus spread occurs early, during the period of activity of the colonizing aphids, before a large apterous population develops (Doncaster and Gregory, 1948; Broadbent and Gregory, 1948; Broadbent, Gregory and Tinsley, 1950). In Canada, too, over half the season's spread of virus occurred when aphids were few (Bagnall, 1953), and in Norway virus Y was mostly spread by the early colonizing winged *Aphis nasturtii* (Kltb.) (Bjørnstad, 1948). Fisken (1959) in Scotland concluded that immigrant alatae could deposit nymphs on several plants. His experiments suggested that apterae played only a small part in spreading the aphid infestation in

potato crops. The lack of virus spread when aphids are numerous during midsummer is partly because potato plants become resistant to infection as they age, and experiments have shown that there is negligible spread from current-season infected potato plants (Heathcote and Broadbent, 1961).

Some reliance can be placed on statistical correlations when they confirm experience. The very significant correlation that I obtained between trapped *Myzus persicae* (Sulz.) and the spread of both leaf roll and Y viruses suggested that most spread was by alatae (Broadbent, 1950). Multiple regressions also suggested that apterae play little part in spreading either virus, a view later confirmed by Hollings (1955) and Neitzel (1962). Multiple regression analyses by Watson and Healy (1953) suggested that winged *M. persicae* were most important in spreading yellows virus in sugar beet crops; wingless *M. persicae* and both winged and wingless *Aphis fabae* Scop. were relatively unimportant.

The use of insecticides has given the most positive evidence in favour of spread by alatae, because it was possible to prevent the development of an apterous population but not the visits by alatae. Emilsson and Castberg (1952) controlled aphids with parathion but not the spread of virus Y. Schepers, Reestman and Hille Ris Lambers (1955) sprayed potato plants with nicotine twice weekly from emergence to death: no apterae were allowed to develop, yet there was considerable spread of both leaf roll and Y viruses, and the distribution of infected plants in treated and untreated plots was similar. It was concluded that spread of both viruses within the field, as well as in to it, was caused by alatae arriving from outside the field; most of the alatae were not infective on arrival.

Good control of leaf roll spread within crops, but not of virus Y, was obtained with insecticides in experiments over several years (Broadbent, Burt and Heathcote, 1956; 1958; 1960). This was because incoming alatae take about two days to acquire and become infective with leaf roll virus, during which time they die after feeding on sprayed foliage, whereas virus Y is picked up and transmitted within a few minutes. The plants must be covered with insecticide for the first few weeks after emergence to achieve control of virus spread, i.e. during initial colonization by alatae. More information on the time of virus spread was obtained by spraying with aphicides during four different periods per season (Burt, Heathcote and Broadbent, 1964). One treatment, spraying frequently from plant emergence to prevent an apterous population developing, controlled leaf roll but not virus Y, indicating that most of the spread of Y was by alatae. In the other three treatments, aphid populations were at first allowed to develop unchecked, and then spraying began on different dates. Most of the leaf roll spread was soon after plant emergence, during the period of colonisation by alatae.

There is no doubt that apterae move from plant to plant, and sometimes carry virus. This was shown when winged and wingless aphids moved voluntarily from caged infected cauliflower plants and were placed on healthy seedlings. Wingless *M. persicae* transmitted less often than winged ones; no wingless *Brevicoryne brassicae* (L.) transmitted cabbage black ring spot virus, although they did cauliflower mosaic virus (Broadbent, 1960).

I maintain that both alatae and apterae spread viruses within crops, and that their relative importance varies with crop, season, aphid species present and the size of the population.

THE SIGNIFICANCE OF APTEROUS APHIDS IN THE SPREAD OF VIRUSES WITHIN AGRICULTURAL CROPS

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Aphid-borne viruses must be spread from field to field by winged aphids, but apterae are often the important vectors within fields. I placed several apterous *Myzus persicae*, infected with Beet Yellows Virus (BYV) and Beet Mild Yellows Virus (BMYV), on eight plants which were fifty yards apart in a field of sugar beet, and examined all neaı by plants for aphids and virus each week (1). The apterae moved very frequently. At the end of the first week two-thirds of them were found on plants other than those on which aphids had been placed, and at the end of the second and third weeks more than 90% of them were on plants which had been free of aphids a week earlier. The aphid spread was followed by similar virus spread. Less than one aphid per plant caused 8 to 16-fold increase in virus yellows in the first month (during which no winged aphids were found), and 60 to 600-fold multiplication of disease within 3 months.

In sugar beet fields, the characteristic patches of infection are caused by apterous *M. persicae*, which are ten times as numerous as winged ones (2), and transmit virus more readily (2), and cannot leave the field.

M. persicae is the important vector of BYV, and *A. fabae* (with sedentary apterae) is unimportant. Although, in the laboratory, *A. fabae* transmits BYV only $\frac{1}{3}$ to $\frac{1}{4}$ as readily as *M. persicae* (3), in the field *A. fabae* produces twice as high a proportion of alates (2, 4), and is often far more abundant than *M. persicae;* therefore if alates were all-important *A. fabae* would be the predominant vector. The reverse is true (5). In virus yellows epidemic years *M. persicae* populations in sugar beet crops have averaged less than two per plant; in July 1963 *A. fabae* populations averaged 195 per plant—and the August yellows count was the lowest ever recorded (Hull).

The control measures which were introduced in 1950 to prevent transmission of virus yellows from beet and mangold seed crops, in which the diseases overwinter, to the root crops, are often useless because the role of apterous *M. persicae* in seed crops has been ignored.

The attained target has been to reduce visible yellows incidence below 1% in autumn of the first year of these crops (6); up to 10% of *visible* infections have been recorded in June of their second year (7). However, at this time these crops often harbour populations of 20-50 apterous *M. persicae* per plant (8), rapidly spreading disease. There is a symptomless incubation period of more than three weeks, during which plants are infective (9), and so these crops may be as infective and as dangerous as if they were completely uncontrolled.

This provides an explanation of the statistics (10) which demonstrate that the seed crop control measures have not reduced the incidence of virus yellows.

My results concerning the spread of virus yellows are relevant to the spread of other viruses—and especially potato leaf roll—by apterous *M. persicae.*

Work at Rothamsted, which has been wrongly interpreted, has shown that the aphid-borne potato viruses are predominantly spread by apterous *M. persicae.* These results may be summarised thus:

(I) Maximum populations of *Aphis nasturtii* are several times as great as those of *M. persciae* (11), and in the laboratory *A. nasturtii* transmits leaf roll about half as readily as *M. persicae* (12). Therefore, one would expect it to be as important a vector—but in years when *A. nasturtii* was abundant and *M. persicae* was scarce the spread of leaf roll was very small (11). This can be explained if apterae are all-important—the apterae of *A. nasturtii*, unlike those of *M. persicae*, are sedentary.

(II) Most of the spread of potato viruses occurs early in the season, before the great peak in abundance of winged aphids (13). Broadbent (14) reported "it is not clear why the spread of disease is correlated with aphids trapped after much of the spread has occurred". His dilemma can be resolved—the numbers of winged aphids are correlated with the size of the earlier apterous population, which spread the disease.

(III) When diseased potato crops were grown alongside healthy ones, there was a steep gradient of infection, and "usually the effect of the neighbouring diseased crop was not noticeable at a

distance of more than 10 or 20 rows into the healthy crop. The amount of disease in distant parts of the healthy crop was not more than one might expect in a crop grown in good isolation" (11). One would expect this if spread is by apterae, but not if it is by winged aphids.
(IV) Isolated potato plants, which could only be infected by winged aphids, acquired 95% of their infections in July, but in nearby field crops 30-40% of the infections occurred in May-June (15).
(V) Broadbent *et al.* (15) conducted field trials for several years, and trapped winged aphids too (13). In 1946 only one-tenth as many winged *M. persicae* were trapped as in 1944 or 1945, and, reflecting this, infections of isolated plants were reduced by 90%—but in nearby field trials the rate of spread of leaf roll and virus Y was not reduced at all, which was good evidence of a different mechanism of spread.

Potato leaf roll is a persistent virus, but virus Y is not, and there is evidence that viı us Y is less dependent than leaf roll on spread by apterae. The transmission characteristics of non-persistent viruses make them more suitable for transmission by winged aphids, and less suitable for transmission by apterae, than persistent viruses. Also, virus Y spreads more rapidly than leaf roll to isolated plants, but in nearby fields the converse was true (15). In Norway, leaf roll incidence was correlated only with *M. persicae*, but virus Y was partly dependent on *A. nasturtii* (16). Systemic insecticides, applied often enough, almost completely stop the transmission of leaf roll, but only reduce the incidence of virus Y by 25-75%, depending on season (17, 18).

In conclusion, the predominant importance of apterae of *M. persicae* in spreading persistent and semi-persistent viruses within sugar beet and potato crops has been established. These apterae also make an important contribution to the spread of non-persistent virus Y within potato crops, and therefore the role of apterae in spreading non-persistent viruses within brassica, lettuce and other crops should receive further study. Some of this work is now in progress at Cambridge.

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SOME LEAFHOPPER PROBLEMS IN THE UNITED STATES

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Curly top virus (CTV), *Ruga verrucosans* Carsner and Bennett affects sugar beets and other crops. Its vector, the beet leafhopper, *Circulifer tenellus* (Baker), probably came from the Mediterranean Region. Not seedborne, and not transovarial in the vector, CTV is perpetuated through tubers of *Solanum tuberosum* L. Multiplication in the vector is questionable. Adult leafhoppers with a full charge of CTV generally remain infective. Tolerance to dilution for transmission of CTV extract from infective leafhoppers is 1:24,000. No cross protection of 12 stable strains of CTV is built up in the vector or in sugar beets, but some occurs in tobacco between CTV and a yellow-vein mutant.

Although the vector can transmit CTV to the plant after only a 1-minute feeding (if CTV has incubated in the vector for 4 hours) the average incubation period is 9·6 days for vector feedings of 1-10 minutes. Susceptible sugar beets become reservoirs for CTV 2-3 days after inoculation by the vector, but incubation in the plant can take from 2-39 days depending on amount of CTV, its strain, stage of vector, temperature, and light. Transmission of CTV to sugar beets in the field is influenced chiefly by time and magnitude of spring influx, size of vector population during summer, the percent viruliferous, size and age of plant at time of influx, and abundance of plant reservoirs in and around fields of susceptible crops. Viruliferous leafhoppers in northerly breeding areas may constitute 0-90 per cent of populations. In Southern Arizona they constitute 5-10 per cent of spring migrants. In sugar beets the proportion viruliferous increases throughout summer. Overwintering females retain infectivity.

The vector breeds in arid and semi-arid areas. Several hundred species of plants serve as reservoirs of CTV, the vector, or both, in the breeding areas as a whole; but only 27 species are really important as winter spring hosts of the leafhopper, 13 as summer hosts, and 14 as hold-over hosts until winter annual hosts germinate in the desert. When these winter annual hosts dry out in spring, the leafhopper moves to agricultural districts.

Leafhopper movements in the spring have been traced from the six principal breeding areas, some for more than 500 miles, to agricultural districts. From northerly breeding areas spring migrations drift into contiguous agricultural districts for a month or more. From southerly breeding areas long-distance migrations move northeastward and northward in distinct spurts lasting only a few days, on two occasions about one month apart. West of the Sierra-Nevada Range in California movements intermediate in continuity, duration, and distance, occur. Some long distance movements from the Rio Grande area may extend northward to Minnesota and eastward to the Eastern Seaboard.

Early season reports of leafhopper abundance in breeding areas aid in adjusting planting dates and cultural practices. Planting resistant varieties of sugar beets and double hills of tomatoes, utilising a beet-free period of 6 weeks during which weed hosts are suppressed, and applying insecticides in fields of seed sugar beets all prevent excessive losses. Direct application of insecticides to other crops usually has not been adequate or practical. However, in the breeding areas of southcentral Idaho and the San Joaquin Valley of California insecticides have controlled the leafhopper before it could move to the cultivated fields. Replacing host plants with a nonhost grass is now being tried on a large scale in breeding areas of southcentral Idaho.

Aster yellows virus (AYV), *Chlorogenus callestephi* Holmes, affects many ornamentals, carrots, celery, flax, lettuce, potatoes, and other crops. The six-spotted leafhopper, *Macrosteles fascifrons* (Stål), is by far the most important of the 24 leafhopper vectors. Of more than 335 plants, about 125 are hosts for both *M. fascifrons* and AYV, 23 for this vector only, and 189 for the virus only.

AYV is neither seedborne nor transovarial in *M. fascifrons.* It overwinters and multiplies in this vector and in perennial, biennial, and winter annuals. The two major strains of AYV are the eastern and the California, the latter of which has at least four variants. Recently one or more of the variants spread eastward to become dominant in Wisconsin. Cross protection of eastern and California strains occurs in *M. fascifrons.* Some cross protection among three

isolates of the California strain occurs in the leafhopper and in plant hosts, but *M. fascifrons* can simultaneously transmit AYV and blue dwarf virus.

Although *M. fascifrons* can acquire AYV in 15 minutes, the per cent infective increases as feeding increases to 8 hours. Minimum vector incubation takes 8-25 days depending on species, strain of virus, temperature, and length of acquisition feeding. Incubation in the host takes 9-50 days depending on plant species, strain of virus, and temperature. Plant incubation is essentially independent of how long and how many vectors feed. The per cent of plants becoming infected depends somewhat upon the numbers of viruliferous leafhoppers and resistance of the plant; infection is generally by individual leafhoppers.

Although in its northern habitats *M. fascifrons* can overwinter in the egg stage and contribute to summer populations, large springtime influxes arrive before a local generation develops. In the North-Central States these migrant adults come 500-1,000 miles from large breeding areas in winter grain centered roughly in South-Central States. Migration starting in April, possibly in March, continues to the north, northeast, and northwest until early June. Distances and directions of movement depend on direction, velocity, and duration of winds coinciding with maturation of leafhoppers and grain. Similar migrations may occur in Northeastern States. In Minnesota influxing leafhoppers seemed more important than local ones in transmitting AYV, possibly because of differences in the per cent viruliferous. In Wisconsin the per cent viruliferous ranged from 5 to 14 in June, soon after the influx, and from 0-1 in September; in New York it was lower; on desert hosts in California it increased from 2 per cent in April to 36 per cent in August.

Varieties of flax and sunflowers resistant to AYV are being developed, but no resistance has been observed in carrots and no source of genetic resistance in lettuce. Some AYV control resulted from roguing diseased plants, eradicating weed hosts, controlling leafhoppers on weeds bordering fields of lettuce and endive, and planting early or very late celery. In 3 years air application of DDT to weed hosts in creek bottom breeding areas adjoining the Aroya Grand Valley, California, reduced AYV in celery from 30 to 5 per cent at low cost. Foliar applications of insecticides markedly increased yield of carrots. Frequent foliar applications of malathion satisfactorily controlled AYV in lettuce. Promising results were also obtained by preplant furrow application of systemic insecticide in lettuce, flax and potatoes.

BLACKCURRANT GALL MITE (*CECIDOPHYOPSIS RIBIS* NAL.); ITS SPREAD AND CONTROL IN RELATION TO THE VIRUS REVERSION

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This Eriophyid mite, the most important pest of blackcurrants is the only known vector of the virus Reversion which greatly reduces yield. Most mites disperse during blossom time and leave galled buds by one of four methods. (Ann. Rep. Long Ashton Res. Sta. for 1959).

If the bud surface is dry and the temperature above 50°F mites leap by muscle contraction and rapid relaxation and are then carried by wind. The rate of leaping increases with increases in windspeed up to 24 miles per hour and this regulation is of great advantage in dispersal since windspeeds within blackcurrant bushes are very low. All air currents assist in the lateral dispersal of mites between bushes and rows but eddies in gusty conditions carry mites upwards well above crop level for wider dispersal.

Mites may crawl away from galled buds and their subsequent behaviour enables many of them to reach the outsides of bushes where their chances of spread to other bushes and of infecting the new buds being formed on the extension growth are increased.

Other mites are transported by various invertebrates, which move over the galled buds and to which the mites attach themselves. Insects are the most common vectors and more mites have been found on aphids than on any other group. Laboratory experiments have indicated that mites can remain attached to insect bodies for many hours and by this method

some long distance dispersal is achieved in addition to that resulting from the general fauna movement within bushes and from bush to bush.

Some mites are dislodged from the outsides of galled buds by rain and carried down shoots towards the bush base where new shoots are growing and many buds are available for infection.

Dispersal by rainwater streams along shoots is most commonly found after sudden showers in the flowering period.

Large numbers of mites disperse from single galled buds, and their spread falls broadly into two types: the initial infection of a plantation and the spread within a plantation.

Almost all mites in the initial infection of a plantation have been either windborne or carried by insects none of which live only on blackcurrants and so by neither method have the mites had any assistance in finding new plantations. A random distribution is almost invariably found and only rarely can a gradient of infection from the source be detected.

The spread within a plantation is most frequently to adjacent bushes and gradients of numbers of galled buds can more often be found. Such spread occurs since most migrants are below bush top level and not in a suitable site for wind dispersal to greater distances. However within a plantation only on bushes within a few yards of the infection source can a clear gradient of numbers of galled buds be found.

No evidence has been found for the theory that mites disperse predominantly in the direction of the prevailing wind. The spread of Reversion virus to healthy plants appears to be more restricted than mite spread and not to follow this closely. This might be explained by the death of some mites after virus transfer and by the inability of others to transmit the virus.

Control measures against the mite have been devised (Ann. appl. Biol. 1962, 50.) based on repeated applications of low concentrations of sulphur compounds which can be used at the blossom stage without hazard to pollinating insects and not presenting toxic residue problems when used at later stages.

THE VIRUS-INDUCED SUSCEPTIBILITY OF BLACKCURRANT BUSHES TO THE GALL MITE VECTOR (*CECIDOPHYOPSIS RIBIS* NAL.)

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The gall mite *Cecidophyopsis ribis* Nal. infests the buds of blackcurrant bushes and prevents the development of true leaves and flowers. It is also important as the vector of reversion virus. This is widespread in Britain and the most virulent strains cause bushes to become virtually sterile.

The relative susceptibility to mites of the main commercial varieties of blackcurrant was assessed in a field trial started in November 1961. One-year-old bushes which were free of mites were exposed equally in a randomised block design alongside reverted bushes with many galls. After two years of unrestricted spread there were significant differences between certain varieties in the number of galled buds found during the winter. However, the most striking feature of the results was that in all instances less than 10% of the buds were infested.

Some features of the natural resistance of blackcurrants to mites became obvious in April, May and June 1964 when shoots of the varieties Amos Black, Baldwin and Wellington XXX were exposed to infestation and dissected at weekly intervals throughout the dispersal period. On each occasion mites were found only on and around the youngest accessible buds, which were in the axils of the almost mature leaves. Younger buds and the apices were less readily accessible as they were protected by the overlapping bases of the subtending leaves. Moreover, the movement of mites towards the apex was impeded by hairy barbs on the leaf bases and by the dense down of surface hairs on the unexpanded laminae, petioles and stems.

Mites which reached axillary buds had great difficulty in penetrating to the meristematic apex and leaf primordia on which they feed and reproduce. Many died on the surface and only 9 of the 377 mites recorded on 27 shoots were inside the buds. The remainder were on

the outside of the buds or on adjacent parts of the stems and subtending leaves. The resistance of the buds was associated with their stage of development. Those which were accessible to mites and which were successfully invaded had two or three recognisable leaves surrounding undifferentiated primordia. Mites were able to crawl between the developing laminae and down to the meristem, despite the difficulty of negotiating the hairy barbs already present at the bases of the developing petioles. The barbs and overlapping leaf scales of older buds made them virtually immune to mites.

These observations suggest that the only buds which become infested are the small proportion on each shoot which are vulnerable during the dispersal period of mites. The oldest buds are in the axils of the scale and transitional leaves and most develop sufficiently early to resist infestation. By comparison, the buds in the axils of the youngest leaves evade infestation because they are inaccessible. This explains the characteristic distribution of galls at the lower nodes of fully extended shoots on healthy bushes (1).

Infection with reversion virus greatly increases the susceptibility of blackcurrant bushes to the mite vector. This was demonstrated in 1963 (2) and confirmed in 1964 when reverted bushes which were free of mites were exposed to infestation. Dissections during the dispersal period revealed many mites on the stem and bud surfaces. Even more mites were inside the apical buds and in the axillary buds of all but the oldest leaves. The ability of mites to reach and to enter such a large proportion of the buds of reverted bushes is associated with the sparse distribution of stem and leaf hairs on reverted bushes compared with healthy ones. This facilitates the movement of mites and their entry into buds and also decreases the effectiveness of the barrier to mites reaching the apex and youngest leaves. Infested apices continue to grow and produce infested axillary buds, so that all but the lowest buds become heavily infested and there is a much more even distribution of galls than on healthy bushes.

The extreme susceptibility of reverted bushes to mites has important implications in experimental design and the health of bushes must be standardised more carefully than hitherto. Experiments on the spread and control of mites may be made particularly sensitive by using reverted bushes, although both healthy and infected ones must be used for a full evaluation of spray materials and methods.

The results also necessitate a reassessment of the direct damage caused by mites and emphasise the critical importance of removing reverted bushes as they occur, if mites and reversion are to be controlled effectively. Virus infected bushes often support a large mite population, impeding control by existing sprays and menacing healthy bushes in the vicinity. By comparison, in isolated plantations where infected bushes are removed promptly, mites are rarely sufficiently numerous to cause a serious problem, and they are vulnerable to chemical control as they fluctuate at a low level which varies with seasonal factors. It seems that the damage caused by mites as vectors of reversion virus is much more important than their effect on buds. Indeed, the direct damage due to mites alone may be insignificant unless infested bushes are rendered susceptible by the effects of reversion virus.

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RELATIONS OF INSECTS TO THEIR HOSTS: (1) VARIETAL DIFFERENCES IN HOST INSECT RELATIONSHIPS

SELECTION FOR COMBINED RESISTANCE IN ALFALFA, *MEDICAGO SATIVA* L., TO PEA APHID, *ACYRTHOSIPHON PISUM* (HARRIS) AND SPOTTED ALFALFA APHID, *THERIOAPHIS MACULATA* (BUCKTON)

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Two species of aphids, the pea aphid, *Acyrthosiphon pisum* (Harris), and the spotted alfalfa aphid, *Therioaphis maculata* (Buckton), are severe pests of alfalfa. Resistance to the pea aphid in alfalfa has been known since 1934 (1, 6) and several varieties have a measurable degree of resistance (2, 4); however, no highly resistant varieties have been released. Resistance to the spotted alfalfa aphid was discovered in Lahonton when this newly introduced pest reached variety tests in southwestern United States. Moapa and Sonora, derived from the variety African alfalfa in California, and Cody, derived from Buffalo alfalfa in Kansas, were recently released to farmers. All are highly resistant to the spotted alfalfa aphid and were produced by selection from each's parent variety.

The primary selection for resistance to both aphids can be made at all stages of plant development but is done most conveniently in the seedling stage (cotyledon and first trifoliolate stages of growth for pea aphid and spotted alfalfa aphid, respectively) (3, 5).

The procedure for breeding a variety resistant to both aphids yet similar to Ladak will illustrate the method being used with several adapted varieties at the Kansas Agricultural Experiment Stations. Approximately 50,000 seedling plants were exposed to many spotted alfalfa aphids in one group and another group was exposed to pea aphids. The survivors, after being repotted and recovering, were exposed to colonization by the respective aphid species. The 80 surviving plants were then planted in an isolated nursery for interpollination and seed production. The seedling progenies were first exposed to killing by spotted alfalfa aphids, then survivors were exposed to the pea aphid and selected for lack of stunting. Plants that survived both infestations were tested for ability to support reproduction by the two aphids. The 103 plants that passed these tests satisfactorily were planted in an isolated replicated, recombination nursery and allowed to interpollinate and produce seed. Resistant seedlings were again selected by allowing pea aphids, followed by spotted alfalfa aphids, to kill all possible plants. Sixty surviving progeny from each clone were inoculated with bacterial wilt and apparently resistant plants tested for ability to support a population of each aphid species, by caging five adult aphids individually on each plant. They were then planted in an observation nursery. The 87 surviving plants of this generation represent one to four plants from each of 29 original parental clones. Equal amounts of polycross seed from each of the 87 plants were mixed and planted to establish a breeder seed field for a synthetic called KS10. Large scale agronomic and further entomological tests are now in progress. Present indications are that the synthetic has many of the desirable characters of Ladak and, in addition, is resistant to both aphids and bacterial wilt. The procedure indicated above required about 5 years.

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THE IMPORTANCE OF STRAINS OF *AMPHOROPHORA RUBI* (KALT.), THE RUBUS APHID, IN THE PROBLEM OF BREEDING FOR RESISTANCE IN THE RASPBERRY

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It is believed that breeding for resistance to insect pests in perennial fruit plants could be of value in reducing the high cost and possible risks associated with spraying, and particularly in eliminating virus vectors which cannot at present be entirely prevented from transmitting disease, by chemical means.

Amphorophora rubi, the rubus aphid, is the vector of several viruses, which the winged forms transmit from plantation to plantation, and which the apterae spread within plantations. The Lloyd George raspberry, which is resistant to the form of *Amphorophora* present in North America, has been widely and successfully used there as a parent in developing locally adapted mosaic escaping varieties.

At East Malling the obsolete British variety Baumforth A and the American variety Chief both originally provided resistance to the culture of aphids originally used (3, 4). Work from 1955 to 1958 (1) revealed the existence of two further strains, numbered 2 and 3, that were capable, respectively, of breeding on plants carrying resistance genes from Baumforth A and Chief. Plants carrying a resistance gene from each variety in combination were, however, able to resist all three strains.

More recent work (2) revealed the presence of a fourth strain capable of breeding on plants carrying this two-gene combination. A further plant gene has been found, however, which will provide resistance to all four strains.

Field surveys showed that strain 2, and particularly strain 4, were uncommon and occurred in close association with the obsolescent variety Malling Landmark, a resistant derivative of Baumforth A still grown in a few places. Strain 3 was common and was found to increase rapidly on varieties resistant to strain 1. The latter strain appeared to be the predominant form. If the Landmark variety were eradicated, resistance to strains 1 and 3 only would be of major importance.

Genetic studies of the aphid strains suggested that the differences between strain 2 and strain 1, and between strain 3 and strain 1 were in each case due to a single mutated gene, the former dominant and the latter recessive, and that strain 4 carried these two mutated genes in combination.

Acknowledgement is made of the close collaboration of the plant breeders at East Malling, Dr. R. L. Knight and Miss Elizabeth Keep, and it is suggested that team research is essential to success in work with insect resistance.

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VARIABILITY OF RESISTANCE OF BARLEY VARIETIES TO THE APHID *RHOPALOSIPHUM PADI* (L.) IN DIFFERENT ENVIRONMENTS

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The three generally recognized mechanisms of resistance in plants to insects are preference or non-preference, antibiosis, and tolerance. Antibiosis and tolerance in barley varieties to the aphid *Rhopalosiphum padi* (L.) have been investigated at the Department of Entomology, University of Manitoba by Hsu and Robinson (1, 2). Forty-three out of 468 varieties tested in the greenhouse and the field demonstrated both antibiosis and tolerance. Wingless females were caged on the plants, and the varieties were classed as showing antibiosis if less than 15 young were produced in five days. In greenhouse and field tests the environment was not controlled.

In subsequent tests in a plant growth room where temperature and light could be controlled more precisely, we were unable to demonstrate antibiosis in terms of reduced aphid fecundity on the 43 varieties of barley formerly classed as resistant. Fecundity is a commonly used measurement of antibiosis, but in order for the measurements to be valid the environment must be strictly controlled. This paper is a review of some of the factors which have been found to influence the reproduction of aphids, by other workers and in our own investigations.

1. The test aphids should be of one morph, preferably the aptera vivipara, descended from a common mother and reared in a standardized environment. They should be of the same age, and tested for reproduction during the first five days of their adult life. Biotypes in aphids have been found by several workers. To avoid possible differences from biotypes it is wise to use in tests a "line" or "clone" of aphids descended from a common mother.

2. Each variety or species of host plant should be grown from a pure line of seed, in a standardized environment, and tested at the same stage of plant growth. In our investigations in field plots, we found differences in number of young produced on plants of the same seeding date, on which aphids were caged for three different periods, June 8-13, 9-14, and 10-15.

3. In both greenhouse and field tests the aphids should be caged on the plants, not only to confine them to the plant, but also to prevent infestation by winged aphids and to exclude predators and parasites.

4. How many plants constitute an adequate sample? Usually the criterion used is the number that can be counted in one day by one person. In indoor tests where the environment may be controlled, tests made on different dates may be comparable in an analysis of data.

5. Temperature has been shown by many workers to affect fecundity of aphids. We found that average numbers of progeny in field plots in 1962 were all less than those on the same varieties in field plots in 1961. In greenhouse tests, in an uncontrolled environment, 83 per cent of the total number of varieties selected for antibiosis fell within a "winter" period of October-May, and only 17 per cent in a "summer" period of April-September.

6. Light and photoperiod have lesser effects on fecundity of aphids. These effects, either increases or decreases, may be partially due to changed chemical conditions in the plant.

7. Nutrition affects fecundity of aphids in various ways. Some of the factors which must be considered are: the differences between young, mature and senescent leaves; auxin content of the plants; suitability or unsuitability of viruliferous plants; and nutrients in the soil.

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ETUDES AU LABORATOIRE DES PHENOMENES DE RESISTANCE A L'EGARD DES OSCINIES OBSERVES CHEZ DIVERSES LIGNEES DE MAIS

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Diverses observations, faites parallèlement au Laboratoire et dans la nature, ont déjà montré qu'il existe, vis à vis de l'action spoliatrice des Oscinies, des différences de comportement des jeunes plantes de Maïs selon l'origine génétique de celles-ci et les conditions dans lesquelles l'attaque se déroule (1) (2) (3).

Toutefois, l'éventail actuel des interactions observées entre Maïs et Oscinies, très ouvert du côté de la sensibilité, l'est beaucoup moins en ce qui concerne la résistance. En fait, on ne connaït pas encore de variétés de Maïs qui soient totalement immunes vis à vis des Oscinies, bien que certaines d'entre elles possèdent indiscutablement des facteurs de résistance dont le généticien doit pouvoir tirer parti.

Mettant à profit: les résultats obtenus au Centre National de Recherche Agronomique sur la sélection de nombreuses lignées de Maïs, et la possibilité que l'on a de reproduire au Laboratoire, sous conditions controlées, divers aspects des relations physiologiques qui existent naturellement entre *Oscinella frit* L. et ses plantes hôtes (2), nous avons tout d'abord démontré que des niveaux très élevés de résistance peuvent caractériser certains Maïs. C'est ainsi que deux des lignées étudiées (Pb 24 et CH 10) ne présentent jamais que de très faibles dégâts et empêchent la majeure partie des larves d'arriver au terme de leur développement. Les taux de survie des Oscinies sont le plus généralement de l'ordre de 0 à 3% pour Pb 24, de 10% pour CH 10, tandis qu'ils atteignent 50% chez les variétés sensibles placées dans les mêmes conditions d'expérience. L'observation précise du comportement des jeunes larves d'Oscinies, ainsi que des vitesses de croissance des Maïs, tend à montrer que ce sont des phénomènes d'Antibiosis et de tolérance qui sont responsables de la résistance de CH 10, tandis que des facteurs d'Antibiosis seuls entrent dans l'immunité de Pb 24.

Cependant, il y a lieu de signaler que chez ces deux lignées, l'appareil foliaire isolé du reste de la jeune plante et mis en survie en boîte de Pétri, ne possède plus ce haut degré de résistance, et permet alors un développement normal des larves. Cela signifie que les facteurs d'Antibiosis dépendent probablement du métabolisme de croissance de la plante.

Utilisant, en outre, des larves des 2ème et 3ème stades pour contaminer artificiellement des plantes de Mais ayant 1, 2 ou 3 feuilles, il est apparu que les stades végétatifs les plus avancés présentent toujours les moins grands dégâts, et sont les plus défavorables au développement des larves, tandis que ces dernières s'accommodent d'autant mieux de leur plante hôte qu'elles sont plus âgées.

Possédant ainsi à la fois des lignées très résistantes et des lignées très sensibles, nous avons cherché à voir comment les facteurs d'immunité se transmettaient dans la descendance par l'analyse des résultats de croisements divers, certains de ceux-ci étant même diallèles. Les conclusions de cette étude sont les suivantes:

1. Le phénomène d'Hétérosis que montrent en général les hybrides obtenus n'est pas capable, à lui seul, de rendre ceux-ci plus résistants. La résistance n'augmente que si le croisement comporte une lignée reconnue initialement immune.

2. Les facteurs de résistance apparaissent comme dominants par rapport aux facteurs de sensibilité, mais il ne parait pas, en première analyse, que leur transmission soit de type mendélien.

3. Dans les deux cas où des croisements réciproques ont pu être effectués, nous avons observé que les caractères de résistance, ou de sensibilité, des hybrides variaient considérablement selon le sens même du croisement.

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RESISTANCE IN *MELILOTUS* TO *SITONA CYLINDRICOLLIS* FAHRAEUS

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The sweetclover weevil, *Sitona cylindricollis* Fåhraeus, is the principal limiting factor in the growth of sweetclover in North America. This paper describes research on weevil-resistance within the sweetclover genus *Melilotus* Adans.

The U.S.D.A. provided us with 162 sweetclover accessions comprising 11 species from 36 countries. These plus 19 varietal or experimental selections of commercial sweetclovers were screened in field trials conducted in 1963.

Evaluation of the comparative resistance to the weevil of the various entries was based on adult feeding preferences as determined by estimation of the percentage of the leaf area consumed. In the cotyledon stage the relative resistance of the plants proved to be independent of their comparative resistance in later development. Once true leaves were acquired the only evidence of changes in the relative resistance among the various entries was that the more vigorous sweetclovers were more tolerant of injury.

None of the accessions proved immune to weevil attack beyond the cotyledonous stage but striking interspecific and intraspecific differences in the relative susceptibility of the various accessions were found. The most resistant entries suffered approximately 1/5 to 1/3 the defoliation of the most susceptible entries.

All entries were evaluated seven weeks after seeding. In the subgenus *Micromelilotus* Suv., the lone entry of *M. infesta* Guss. was only 18% defoliated; the 9 entries of *M. sulcata* Desf. ranged from 33-63%; 5 entries of *M. messanensis* All. from 55-61%; 3 entries of *M. italica* Lam. from 58-66% and 32 entries of *M. indica* All. from 72-83% defoliated. In the species of the subgenus *Eumelilotus* Suv. screened the 6 entries of *M. dentata* Pers. ranged from 49-58% defoliated; 46 entries of *M. alba* Desr. from 58-75%; 69 entries of *M. officinalis* Desr. from 59-78%; and two entries of *M. suaveolens* Ldb. from 76-78% defoliated.

While it is possible that an intensive search in large populations of *alba* and *officinalis* may locate plants or mutants having a significant level of resistance, our observations appear to indicate that the most promising approach may be to attempt to transfer weevil-resistance from other more resistant species to the agriculturally important species.

It is in certain species of the subgenus *Micromelilotus* that the greatest level of resistance was found. To date the feasibility of crosses between species of the subgenus *Eumelilotus*, to which our agronomically important species belong, and species of the subgenus *Micromelilotus* has not been demonstrated. *M. dentata* perhaps provides the most accessible source of an appreciable level of weevil-resistance; all 6 entries of this species were more resistant than any of the white or yellow sweetclovers. The feasibility of crosses between *dentata* and *alba* has been demonstrated in the development of coumarin free sweetclovers. Crosses between *alba* and *officinalis* have also been made although both involve special breeding techniques.

ANALYSE DANS LES CONDITIONS DU LABORATOIRE D'UN EXEMPLE DE RESISTANCE VARIETALE D'AVOINE VIS A VIS D'UN DIPTERE *HYDRELLIA GRISEOLA* FALL. (EPHYDRIDAE)

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Hydrellia griseola Fall est un petit diptère Ephydridae dont la larve mine les feuilles d'un très grand nombre de Monocotylédones herbacées appartenant aux familles des graminées, alliacées etc. (1, 2).

Des études préliminaires nous ont montré que, chez une même espèce végétale, des différences variétales du comportement vis à vis d'*Hydrellia* pouvaient exister. C'est ainsi que chez dix variétés cultivées d'Avoine, les possibilités de développement d'*Hydrellia griseola* varient de 1 à 160, la plus défavorable étant "Noire du Prieuré" et la plus favorable "Victoire".

Des différences corrélatives dans les durées moyennes du développement larvaire et dans le poids frais moyen des jeunes pupes sont également observées.

L'analyse expérimentale, que nous avons tenté de faire, porte sur deux variétés cultivées d'avoine l'une très résistante "Noire du Prieuré", l'autre très sensible "Noire de Moyencourt". Elle concerne l'incidence sur le développement d'*Hydrellia*, des caractères de végétation sous des conditions différentes de photopériode et de nutrition, ainsi que des particularités morphologiques, histologiques et biochimiques.

Bien qu'il n'ait pas été possible de mettre en évidence un caractère qui puisse être rendu responsable des différences variétales observées, cette étude nous permet cependant de dégager plusieurs conclusions.

1. D'une façon générale les variétés d'hiver se montrent très nettement les moins favorables au développement d'*Hydrellia griseola*. Cela peut indiquer une relation entre la résistance au froid et la résistance vis à vis de ce diptère, ainsi que l'intervention corrélative de facteurs physico-chimiques propres à ces variétes.

2. Le caractère de résistance, indépendant des structures morphologiques et histologiques, parait en outre échapper à l'action des facteurs climatiques et édaphiques. Il se révèle principalement par l'impossibilité dans laquelle se trouvent les jeunes asticots de continuer leur développement, ce qui suggère l'existence d'un phénomene d'*antibiosis*.

3. L'observation précise du comportement d'installation et d'alimentation des jeunes larves ainsi que des réactions des plantes attaquées, montre qu'il existe des différences très nettes selon le degré de sensibilité ou de résistance de la variété, ce qui fait penser à une nature d'ordre chimique des facteurs d'antibiosis, et même, plus probablement, d'ordre enzymatique. Il se peut en effet que l'action des enzymes protéolytiques de la larve soit plus ou moins inhibée lorsque celle-ci s'attaque aux variétés resistantes.

4. Les dosages chimiques effectués essentiellement sur les substances primaires de la feuille, ne permettent pas de distinguer la variété résistante de la variété sensible.

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SUR L'ADAPTATION D'UN INSECTE NUISIBLE A UNE CULTURE: *DREPANOTHRIPS REUTERI* UZEL SUR VIGNES FRANCAISES

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Parmi les nombreuses espèces nuisibles à la vigne, deux seulement sont originairement inféodées à cette culture, le Phylloxera et un buprestidae, *Agrilus derasofasciatus* Lac. Les autres (Eudemis, Cochylis, Pyrale, Altise, Cigarier, Gribouri etc. . . .) se sont adaptées secondairement. *Drepanothrips reuteri* Uzel (Thysanoptère Terebrant) est dans le même cas. Insecte polyphage vivant sur Hêtre, Chêne, Noisetier, Saule, et même *Cistus monspeliensis* il est signalé en 1911 par Pantanelli comme causant des dégâts exclusivement sur vignes américaines. Nous l'avons observé (A. Bournier 1957) comme nuisible dans le Languedoc méditerranéen aux cépages hybrides franco-américains (12·375, 18·315 en particulier) puis il est passé sur vignes françaises (Cinsaut, Carignan, Chasselas) (A. Bournier 1962).

Sur les vignes américaines (*V. riparia* et *V. rupestris*) ainsi que sur leurs hybrides les dégâts présentent à peu près la même apparence. Les femelles sortent d'hivernation au moment où les bourgeons éclosent. Elles piquent les jeunes feuilles causant ainsi des nécroses du limbe. Au cours du développement ces parties desséchées tombent. Plus tard des piqûres sur les pédoncules floraux provoquent du millerandage ou une coulure parfois considérables. Sur le méristème apical les piqûres atteignent des cellules qui donneront des tissus plus profonds, en particulier le cylindre central. Le sarment est alors peu vigoureux, les mérithalles courts, les feuilles plus petites: le dégât rappelle beaucoup le court-noué.

Nous n'avons pas encore pu déterminer s'il s'agit d'une toxémiase ou si, les cellules des vaisseaux étant lésées, la mauvaise circulation de la sève est responsable de la nanisation des sarments. Mais la luxuriance des hybrides efface ce retard en six semaines.

Il en est autrement sur vignes françaises (Cinsaut). Le méristème attaqué donne un sarment qui n'atteint que le quart de sa longueur normale. Sur le bois de deux ans partent aussi des sarments nains. Le flux de sève, freiné par l'obstruction des vaisseaux cherche un exutoire dans le départ de bourgeons sur le vieux bois. Le bras atteint périclite, il est supprimé au cours de la taille d'ou déséquilibre puis mort de la souche. Nous avons ainsi assisté à la disparition de vignes entiéres.

Sur les côteaux, la végétation s'arrêtant tôt, les thrips ne font pas d'autre dégât. Mais dans des terrains humides la végétation tendre des bourgeons axillaires permet la pullulation des insectes. Les piqûres sur limbe donnent aux feuilles un aspect tourmenté, l'épiderme des baies est subérisé comme le ferait une violente attaque d'oïdium, empêchant la maturation du raisin.

Ces dégâts sur vignes françaises n'avaient jamais été observés en France ou en Italie. Plusieurs hypothèses peuvent être formulées pour expliquer cette adaptation.

1° La vogue grandissante depuis 20 ans des hybrides producteurs directs a-t-elle permis la sélection de races qui sont passées ainsi peu à peu des vignes américaines aux vignes françaises en utilisant leurs hybrides comme transition?

2° Les pullulations enregistrées sur les vignobles de terrains humides pourraient être dues à l'action de certains pesticides (cas parallèle des *Eotetranychus*). Le conditionnement de certaines matières actives (adjuvants, mouillants, etc. . . .) pourrait être en cause et agir soit par destruction des prédateurs naturels, soit par modification du chimisme des tissus végétaux entrainant une augmentation de la fertilité de l'insecte.

En l'état actuel de nos recherches nous sommes obligés de nous borner à la constatation de ce phénomène d'adaptation d'un nouvel insecte nuisible aux vignes françaises. Nous espérons que l'explication, bien que difficile, pourra être donnée prochainement avec plus de certitude.

(2) NUTRITION OF PHYTOPHAGOUS INSECTS IN RELATION TO HOST-PLANT COMPOSITION

NUTRITION OF PHYTOPHAGOUS INSECTS

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Plants contain many substances that are not used as nutrients by insects. To determine dietary requirements of phytophagous insects, the nutritive substances must be separated from all others that influence insect behavior and physiological development. The composition of plants varies with nutrition, age, temperature, day length, light quality, soil, and altitude; therefore the dietary requirements of insects are not easily determined. The effect of food on the insect becomes even more complex for insects that feed on different plants or different parts and varieties of the same plant species. Also, there are odorous substances that attract insects to certain plants although unrelated plants might provide enough nutrients if the insect were induced to feed upon them.

To avoid the complicating environmental factors and the plant substances that are eaten but not utilized by insects, artificial diets that can be reproduced easily have been used to rear insects and study their dietary requirements. In addition to supplying nutrients, a good rearing diet should give a 70 per cent or more yield of adults from eggs or immature forms. The size and rate of development of the insects should be similar to those of insects grown in their natural environment. Adults should mate and lay viable eggs. In our laboratory, good rearing diets were developed for the boll weevil, *Anthonomus grandis* Boheman, the pink bollworm, *Pectinophora gossypiella* Saunders, the bollworm, *Heliothis zea* Boddie, the salt-marsh caterpillar, *Estigmene acrea* Drury, and several other insects.

Diets for many insects should include the following ingredients; either protein or amino acids, a carbohydrate (usually a simple sugar), unsaturated fatty acids, a sterol, choline, inositol, minerals, B-vitamins, ascorbic acid, fat soluble vitamins, water, and inert substances to thicken or stabilize the mixture. Satisfactory diets for many insects have been prepared by combining pure chemicals with some plant preparation or other natural product. However, the only way to determine the nutrients or regulate their concentrations without performing analyses upon the insect or its food is to devise diets having all constituents of known composition. Impure chemicals frequently contain trace nutrients that are not detected when nutritional experiments are performed.

Occasionally an insect does not grow or reproduce when fed complete diets that are either defined or contain natural substances. There may be several reasons for this. Feeding may be prevented by a dietary constituent that is not present in the insects' natural diet. Also, in the preparation of extracts of natural host plants, substances may be changed so that their inherent attractiveness is destroyed. Furthermore, an insect may not grow if the nutrients are not properly balanced.

With defined diets qualitative and quantitative requirements for the nutrients can be determined in deletion experiments. In the insect's relationship to a plant, quantitative data may be very useful in predicting whether a plant variety is deficient in a nutrient that is vital to growth. After the dietary requirement for a substance has been determined, the amounts needed can be correlated with the amounts of the nutrient contained in the plant. For example, the amount of ascorbic acid in the boll weevil is high in the adult and in the egg when the adult is feeding on fresh intact cotton fruit. During larval and pupal stages, the content of the vitamin in the insect decreases. The amount in the food also decreases because the fruit usually falls off the plant or deteriorates.

Most phytophagous insects that have been studied have specific requirements for a large number of nutrients. During the evolutionary process these insects probably lost the ability to synthesize vital compounds because of the abundance of nutrients provided by plants.

A PROPOS DE LA BIOLOGIE D'*ARCTIA CAJA* L. (LEPIDOPTERES—ARCTIIDAE)

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Arctia caja L., Lépidoptère Arctiidé, est un insecte très polyphage. On rencontre ses chenilles sur de nombreuses plantes basses herbacées, et aussi sur certains arbres ou arbustes. Du point de vue économique, les dégâts causés à la vigne en début de végétation peuvent prendre occasionnellement une grande importance.

Le présent article traite de l'influence de l'alimentation sur le développement de l'insecte, de l'action particulière du feuillage de Vigne, et enfin d'essais d'alimentation sur milieu artificiel semi-synthétique.

Les chenilles proviennent de pontes récoltées soit au mois de Juin, soit au mois de Septembre. En effet, dans nos régions, l'insecte présente deux générations par an, ou plutôt une génération complète et une génération partielle, l'hivernation s'effectuant dans la plupart des cas au 5 ème stade larvaire; le nombre des stades est normalement de 7.

Les élevages s'effectuent à la température de 22 à 24°C, et sous éclairage constant fourni par des tubes "Phytor". Une souche a pu être maintenue sur Plantain, de sorte que certaines expériences ont fait appel à des insectes de 2ème, 3ème ou 4ème génération.

La polyphagie des chenilles d'*Arctia caja* leur permet de consommer des nourritures plus ou moins favorables à leur croissance. Parmi les diverses plantes proposées, on peut distinguer des aliments très favorables, comme *Plantago lanceolata*, certains un peu moins favorables, comme *Salix viminalis* et *Urtica dioica*, d'autres permettant des résultats moyens, comme *Rubus idaeus*, *Ligustrum vulgare*, *Salix caprea*, *Malus communis*, d'autres enfin nettement défavorables.

Parmi ces derniers, il en existe certains, comme *Populus nigra* et *Populus alba*, sur lesquels les chenilles s'alimentent faiblement, restent de petite taille, mais survivent longtemps en effectuant 6 ou 7 mues. Si on remplace le Peuplier par une nourriture favorable, les insectes comblent le retard accumulé en une ou deux mues seulement. Sur *Vitis vinifera*, au contraire, la consommation est relativement importante pendant les premiers jours, mais ensuite elle diminue, la mortalité apparait après une semaine environ, pour atteindre 100% au bout d'un mois. Cependant, dans un cas seulement, un individu a accompli un développement normal sur vigne.

Les essais d'élevage sur milieux artificiels semi-synthétiques ont donné les résultats suivants:

Sur le milieu à base de carotte utilisé pour *Ceratitis capitata* Wied., la croissance est très faible, et on observe rapidement consommation des mues et cannibalisme, phénomènes retardés par l'addition de glucose. Le fait d'ajouter de la poudre de vigne séchée ayant augmenté la survie et supprimé le cannibalisme, c'est la Vigne seule qui est à la base du milieu finalement retenu, dont la composition est la suivante:

Poudre de feuille de vigne	1,0 g
Poudre de cellulose	1,0 g
Gélose	0,2 g
Extrait de levure	0,12 g
Acide benzoïque	traces
Eau distillée	9,5 g

La dessiccation des feuilles de *Vitis* fait donc disparaître leur toxicité.

Parmi les faits mis en évidence, l'un des principaux est que chez *Arctia caja*, il n'y a pas de relation nette entre la prise de poids et la mue. Le nombre et le rythme des mues paraissent assez bien déterminés. Selon l'alimentation fournie, on peut obtenir d'une part plusieurs mues sans prise de poids notable, et d'autre part une croissance très importante avec un petit nombre de mues. Enfin, des chenilles de taille suffisamment grande, placées sur alimentation défavorable, ou tout simplement privées de nourriture, réagissent souvent par une nymphose précoce. On retrouve donc, chez *Arctia caja*, des réactions semblables à celles signalées chez *Tineola biseltiella* et *Tenebrio molitor*.

ISOLATION OF COMPONENTS FROM THE ROOTS OF ALFALFA (*MEDICAGO SATIVA* L.) TOXIC TO WHITE GRUBS (*MELOLONTHA VULGARIS* F.)

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I. *Introduction.* In spite of the well known polyphagous habits and voracity of the white grubs, great differences in susceptibility may be observed among different legumes occurring in meadows or grown as forage crops. We found strains and varieties resistant to this pest in alfalfa and red clover. In grassland heavily infested by white grubs single plants resistant to the attack were collected. In order to eliminate host evasion each plant was exposed in a concrete pipe to white grubs in numbers sufficient to simulate heavy infestation. The progeny of surviving plants was again tested for the heritability of resistance (3).

II. *Feeding Experiments.* The effect of feeding of white grubs on the roots of resistant alfalfa strains was studied by means of preference tests or forced feeding. In the experiments of the first type white grubs were exposed singly to groups of root slices consisting of several varieties or in combination with dandelion (*Taraxacum officinale* L.) as a comparison and standard food. In the other set of experiments the white grubs had no choice between food types. Attempts were made to isolate the factors responsible for antibiosis of resistant alfalfa strains by extracting the roots with water, ethanol, acetone and benzene. Extracts and residues were added to vermiculite and exposed to white grubs with or without dandelion. White grubs of the first and second larval stage—33 to 66 in each group—were exposed to feeding and observations were extended over several weeks, months or even years with larvae of the third stage. Every ten days the white grubs were inspected and the food replaced. Weight increase, number of moulted larvae and mortality of the white grubs were recorded (2).

III. *Results.* The results of four feeding experiments carried out from 1960 to 1964 are reported:

In the first test a clear preference was evident for dandelion in presence of alfalfa roots. Three resistant strains "Oerlikon 91, 92, 93" were selected. No larvae moulted and mortality was highest when fed with roots of these strains exclusively. However white grubs which had access to both alfalfa and dandelion, consumed more dandelion and a higher number of moulted larvae as well as a lower mortality were recorded in the groups fed with both alfalfa and dandelion. In the second experiment white grubs were forced to feed on extracts of two commercial varieties of alfalfa, a Hungarian variety "MV 129", resistant to white grubs, and a susceptible German variety "Frankenwarte". Dandelion was included as comparison and supplementary food. Mortality was highest in the groups fed with water extracts of the Hungarian variety and in the groups fed with alcohol extract of the German variety. The resistant "MV 129" variety exhibited the highest toxicity in the water extract.

In the third feeding experiment extracts were made of the most resistant strain "Oerlikon 93", of the susceptible "Frankenwarte" and of dandelion. The extracts as well as the residues were fed. Mortality was higher in the group fed with extract with dilute ethanol of the resistant "Oerlikon 93" than with that of "Frankenwarte". The residue after extraction with dilute ethanol still exhibited a high mortality indicating that not all antibiotic factors have been removed. The residues of all extractions induced a higher mortality when fed without the roots of dandelion as a supplementary food than when fed together.

Based on the differences obtained in weight increase, number of moults and mortality the resistant alfalfa strain "Oerlikon 93" must have quite a different chemical composition from that of the susceptible "Frankenwarte".

In the fourth feeding experiment the extracts with water and the residues of the resistant strain "Oerlikon 93" were compared to that of dandelion. Weight increase was highest in the group fed with fresh dandelion and least in the group fed with dried alfalfa roots or with the extracts of "Oerlikon 93". Number of moulted larvae was least in the group with dried alfalfa roots whereas the extracts and residue of "Oerlikon 93" were slightly less toxic than dried alfalfa roots.

Additional observations on different chemical composition of alfalfa varieties were obtained by extracting the resistant selection "Oerlikon 93" and the susceptible "Frankenwarte" with dilute ethanol and by shaking for 15 seconds and leaving to settle for 15 minutes.

The foam on the extract of the resistant selection persists for hours or days whereas the extract of "Frankenwarte" produces only little of a weak foam. When cholesterol is added to this extract a substantial precipitation is produced only with the extract of the resistant selection "Oerlikon 93".

Foaming properties of alfalfa is at present being studied at several laboratories in relation to saponin content and bloat promoting potential in cattle (1).

IV. *Discussion.* The question arises whether the insecticidal property of the roots of the resistant alfalfa has to be attributed to a poison or to a deficiency. The hypothesis of poison is sustained by the fact that mortality is higher and weight increase lower in the groups fed with the extracts of resistant alfalfa strains. Weight increase is greater in the groups fed with residues. When we compare two different alfalfa varieties, the resistant one is more toxic than the susceptible mainly in the water and alcohol extracts. The hypothesis of deficiency on the other hand is refuted by a higher mortality in the groups fed with residues of the aceton extract of the resistant selection. As a further explanation we are studying also the hypothesis of blocking: presumably saponin occurring in the resistant strain may block some lipid fraction essential for the development of the white grub.

V. *Summary.* Earlier tests demonstrated antibiosis and tolerance to white grubs in roots of several alfalfa strains. Non-preference was also evident. From the results of feeding tests with extracts from alfalfa roots on vermiculite together with a supplement food it is concluded that antibiosis is due to the higher saponin content of the resistant strains.

VI. *Acknowledgement.* This research is financed by a special grant by the Division of Agriculture of the Department of Public Economy of the Swiss Federal Government. I am much indebted to Dr. F. Bachmann, chemist at the same Experiment Station for preparing the extracts and residues for our feeding experiments.

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PHYSIOLOGICAL FACTORS GOVERNING SUSCEPTIBILITY-RESISTANCE OF PLANTS TO RED COTTON BUG (*DYSDERCUS KOENIGII* F.)

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Under identical phenological, geographical and ecological conditions, differences in the susceptibility or resistance of plants to *Dysdercus* are determined by physiological factors which operate in four phases. The factors operating in the first phase determine the insect's arrival on a plant and its stay on it. When the insect is desiccated it is attracted to almost all the plants tested in response to hygrostimuli emanating from the succulent parts like leaves, unripe fruits, etc., from which it sucks the sap. As the water content of the insect increases due to ingestion of plant sap, its feeding is inhibited and finally stops. The insect then searches for a dry zone. On the susceptible, malvaceous plants an olfactory chemical attractant in the leaves prevents the insect from moving away from the plant and may even attract the insect from a short distance. On these plants, negative hygrotropic response leads the non-desiccated insect to dry, open fruits. Nonmalvaceous plants lack the attractant and the insect moves away.

In the second phase, certain olfactory and gustatory chemical stimulants of the seeds of malvaceous plants induce the insect to initiate and continue ingestion of food. The seeds of less susceptible malvaceous plants have a mechanical barrier and lesser concentration of the chemical feeding stimulants than the seeds of highly susceptible plants like cotton and okra. However, in the absence of these in the fields, the insect can ingest small quantities of food from the seeds of less susceptible malvaceous plants and even from nonmalvaceous seeds.

In the third phase, various factors determine the degree of utilisation of the ingested food. Almost all the nutrients present in the ingested food from the leaves or seeds of the malvaceous

plants are digested, absorbed and metabolised by the insect. It is not so with the nonmalvaceous plants. For instance, whatever little food is ingested from wheat seeds contains carbohydrates mainly in the form of starch which cannot be digested by the insect and is excreted unutilised. This would consequently lead to failure to grow and reproduce.

In the fourth phase, factors involved are those which determine the degree to which the chemical constituents of the utilised food satisfy the metabolic requirements of the insect. All the latter are satisfied by food ingested from cotton and okra seeds, but those of hollyhock and *Abutilon* do not satisfy the lipid requirements. Nonmalvaceous plants, e.g. wheat, are unable to satisfy carbohydrate and lipid requirements.

NUTRITIONAL REQUIREMENTS OF THE APHID, *MYZUS PERSICAE* (SULZ.) IN RELATION TO THE SUITABILITY OF HOST PLANTS

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Since *M. persicae* can be reared from new-born larvae to adults on synthetic diets imbibed via membranes of stretched parafilm, its nutrition can be investigated by studying growth on diets lacking particular components. Such studies showed that sugar is essential for larval survival, and that an amino acid mixture, K, Mg, and phosphate are essential for appreciable growth to occur. Optimal concentrations of these components in synthetic diets have been worked out. Omission of other dietary components (vitamins and sterol) had little effect on the growth of larvae born to adults within a day of removal of the latter from culture plants; but larvae born after their mothers had been maintained for several days on vitamin-deficient diet were then found to require dietary vitamins for satisfactory growth. Evidently certain vitamins are essential, but normally are derived in sufficient quantity from the mother to allow larval growth.

Adults also require sugar to survive longer than the 2-3 days possible on water alone. On 15% sucrose solution they survived up to 12 days and deposited, on average, about 10 larvae. On complete diet having sucrose at the optimal concentration of 15%, adults survived 3 weeks and deposited 20-30 larvae. With amino acids omitted, longevity was unchanged but only about 10 larvae per adult were deposited, much as on sucrose alone. Omission of salts slightly reduced longevity and numbers of larvae, but no such affects were detected on vitamin deficient diet.

A complementary paper deals with phagostimulatory effects of constituents of the diets. It is pertinent to note that phagostimulation depends primarily on sugar, and secondarily on amino acids, other constituents being without marked effects. This may be related to the essentiality of sugar for survival, and the necessity of amino acids for growth and larviposition. Amino acids alone had no phagostimulatory effect, complementing the nutritional finding that diets complete but for sugar sustain survival no longer than water alone.

In designing the synthetic diet, gross proportionalities of the main components were based on available analyses of phloem sap in the literature. These show the principal solutes to be sucrose, at concentrations mainly between 5-20%, and amino acids, as much as 2% in concentration, and sometimes with marked seasonal fluctuations. Since sucrose and amino acids account for most of the sap solutes, it is no surprise to find that these are, in fact, of prime importance both nutritionally and as feeding stimulants.

Having optimal or minimal values for the concentrations of the components of synthetic diets which directly determine survival, growth and larviposition, it becomes possible, by comparing these with the available data on phloem sap concentrations of the same components, to speculate more fruitfully on the likely effects of variations in natural sap concentrations on growth and reproduction in nature. In general, optimal dietary concentrations for sucrose, total amino acids, K, Mg and phosphate are in the ranges of concentrations reported in the literature. Insofar as concentrations for different plant species vary widely for sucrose and amino acids (for which most information is available), and concentrations of amino acids are known to vary seasonally in some plant species, it is altogether likely that such fluctuations could account, in part, for differences in growth and larviposition as between different kinds of plant, or between different seasons on the same plant.

REACTIONS OF FOUR BIOTYPES OF CORN LEAF APHID, *RHOPALOSIPHUM MAIDIS* (FITCH) TO DIFFERENCES IN HOST PLANT NUTRITION

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Application of various fertilizers to plants has been demonstrated to influence insect populations. Effects of nutrient solutions deficient or high in nitrogen, potassium and phosphorus on fecundity and weight of corn leaf aphid biotypes were investigated.

Materials and Methods. Origin of the four biotypes has been indicated by Painter and Pathak (2). A complete nutrient solution (1) with slight modification was used as a standard. Experimental variations stemmed from this standard. Reno barley was sown in flats containing vermiculite to which each nutrient solution was added on alternate days. After a lapse of seven days following germination, plants were maintained in hydroponics in the respective nutrient solutions. Five last instar nymphs of alate aphids were confined on each seedling by a transparent ventilated plastic box. Total living aphids and individual weights of alate aphids were recorded ten days after being caged.

Results and Discussion. Great differences in populations were developed by the four biotypes on Reno barley grown on seven different nutrient solutions. In general, biotypes responded negatively to any change from the complete nutrient solution. Maximum significant differences between biotypes occurred with solutions high in nitrogen. Minimum significant differences were found with the complete solution, a solution low in nitrogen, and a solution low in phosphorus.

Solutions low in nitrogen, significantly reduced populations of KS-1, KS-3 and KS-4 compared with populations on complete nutrient solution. Higher levels of nitrogen had a differential effect on three biotypes. Solutions low in potassium and in phosphorus had nearly identical effects on the four biotypes. Solutions high in potassium significantly increased populations of KS-1 and KS-4 and significantly reduced populations of KS-2 and KS-3, compared with their complete nutrient solution populations. Significant reductions of all biotypes occurred with solutions high in phosphorus compared with complete nutrient solution.

Highest populations of KS-1 were on plants grown in the solution high in nitrogen; of KS-2 and KS-3, on standard nutrient solution; of KS-4, in the solution high in potassium.

There was no apparent correlation between the size of population produced and weight of aphids. Significant differences in body weights between biotypes were found on different nutrient solutions. Significant differences were found in body weights of individual biotypes when reared on barley in complete nutrient solution, compared with the same biotype's body weight reared on barley in other solutions. In general, all the biotypes had significantly heavier body weights on plants grown in complete nutrient solution than on plants grown in the other nutrient solutions.

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DIE BEZIEHUNG ZWISCHEN DEN RÜBENBLATTLÄUSEN *APHIS FABAE* SCOP. UND IHREN HAUPTWIRTSPFLANZEN

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Die Resultate unserer zahlreichen chemischen Analysen der Spindelbäumeblätter und *Beta vulgaris,* die zugleich mit der Beobachtung der Populationsdynamik von *Aphis fabae* durchgeführt wurden, die Entwicklung der Blattläuse *Aphis fabae* jene Blätter am geeignesten sind, bei denen das Inhaltsverhältnis der Zuckerstoffe und des gesamten Stickstoffes in der Trockenmasse der Blätter niedriger als 1 ist. Umgekehrt gesehen, überwiegen in der Population alate Formen und die Fruchtbarkeit der Blattläuse fällt. In dem Zeitabschnitt, wenn das Verhältnis der zwei angeführten Nutritivkomponente einen höheren Wert als 1,3 erreicht, kommt es beim Auftıeten der Blattläuse zur Retrogradation.

Da das Inhaltsverhältnis der stickstoffhaltigen Stoffe und Zuckerstoffe sich im Verlaufe der ontogenetischen Entwicklung nach und nach zu ungunsten der Blattläuse ändert, sind bei Pflanzen bestimmte Entwicklungsphasen, wo die Pflanze sich nicht für weitere Ernährung der Blattläuse eignet. Bei *Evonymus europaeus* verlaufen diese Anderungen ziemlich schnell. (Abb. 1 und 2). Sie beiten den Rübenblattläusen Aphis fabae nur in der Phase des Blattwachstumes eine entsprechende Nahrungsquelle. Dadurch wird im Frühling ausser den Fundatrices nur noch zwei fundatrigenen Generationen die Entwicklung ermöglicht. Aus denen entwickeln sich schon in der Population der ersten Fundatrigenen mehr als 95% alater Formen.

Bei *Beta vulgaris* ändert sich das Verhältnis der angeführten zwei Grundnahrungskomponente zu ungunsten der Rübenblattläuse viel langsamer. Dies ermöglicht *Aphis fabae* auf der Zuckerrübe 6-7 virginogener Generationen zu entwickeln. Die Zuckerrübe bietet die besten Bedingungen für die Entwicklung von *Aphis fabae* in dem Zeitabschnitt der II. und III. Phase ihrer Entwicklung, wen sich der 2.-12. Rübenblatt entwickelt. (Abb. 3 und 4).

In diesem Zeitabschnitt ist die Steigerung der Populationsdichte am intensivsten und in den Populationen überwiegen aptere Formen. Mit dem Übergang der Zuckerrübe in die IV. Phase der ontogenetischen Entwicklung beginnt eine schnelle Änderung der chemischen Zusammensetung der Blattsäfte zu ungunsten der Blattläuse. Dadurch kommt es zur Minderung der Kapazität eines entsprechenden Entwicklungsmilieu der Blattläuse, obzwar die Blattfläche grosser wird. In den Populationen der Blattläuse beginnen die Nymphen der zunkünftigen beflügelten Formen zu überwiegen und die Steigerung der Populationsdichte wird langsamer. Wenn das Verhältnis des Gesamtinhaltes von Stickstoff und Zucker einen höheren Wert als 1,3 aufweist, d.i, in dem Zeitabschnitt, wenn die Rübe mehr als 20 Blätter hat und in der Rübenblattlauspopulation die VI. virginogene Generation auftritt, kommt es in der Gradationskurve zum Beginn der Retrogradation.

Nach der Beendigung der Gradation in den Beständen der Kulturpflanzen kommt es infolge ungünstiger klimatischen Bedingungen in den späten Sommermonaten beim Auftreten der Rübenblattlaus *Aphis fabae* zur bestimmten Depression. In diesem Stadium liegt der Brennpunkt der Populationen in den Unkrautpflanzen, welche den Rübenblattläusen Zufluchtstätte in jenem Zeitabschnitt bieten, wo die Kulturpflanzen keine entsprechende Nahrungsquelle sind. Diese Zufluchstätte ist ein Reservoir, wo sich ausser weiteren 4-5 virginogenen Generationen auch beflügelte Herbstformen entwickeln. Aus den Unkrautpflanzen, besonders die Pflanzen der Familie Chenopodiacae bieten die Nahrungsquelle, und zwar wieder nur junge sich entwickelnde Pflanzen und jene, welche genügend mit Wasser versorgt sind.

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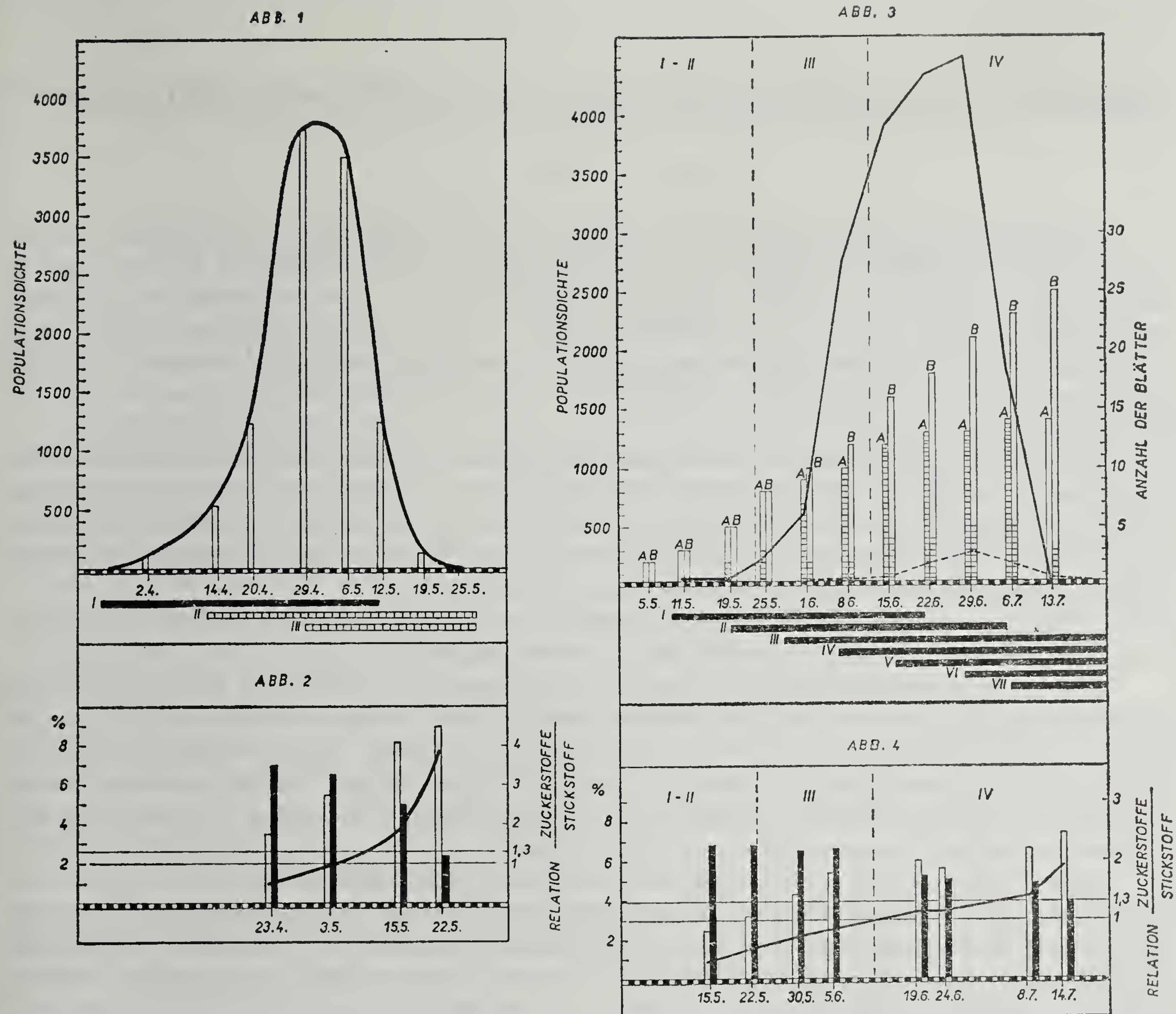

Abb. 1-4. (1) Verlaufes des Gradations- und Generationszyklus der Rübenblattlaus am Spindelbaum; an der Achse X sind die Kontrolltage, an der Achse Y die Populationsdichte der Blattläuse an zwanzig einjährigen Zweigen von einem Spindelbaum. In dem Gradationszyklus ist der Zeitabschnitt des Vorkommens und die Vertretung enizelner Generationen in der Blattlauspopulation dargestellt. - Fundatrices; - Fundatrigenien.

(2) Inhaltsänderungen des Gesamtstickstoffes und des Zuckerstoffes in den Blättern des Spindelbaumes; an der Achse X sind die Tage der chemischen Analysen, an der Achse Y links % Inhalt des Gesamtstickstoffes und der Zuckerstoffe in % der Trockenmasse, rechts das Verhältnis der gesamten Zuckerstoffe: der gesamte Stickstoff. - Zuckerstoffe; - Stickstoff; - Veränderungen im Gesamtzuckerstoffeverhältnis: Gesamtstickstoff.

(3) Verlauf des Gradations- und Generationszyklus der Rübenblattlaus in den Zuckerrübenbeständen; an der Achse X sind Kontrolltage, an der Achse Y die Populationsdichte, rechts die Anzahl der Blätter. Unter dem Gradationszyklus ist der Generationszyklus dargestellt. - Wachstum der Populationsdichte an den initial befallenen Rüben (A); - Wachstum der Populationsdichte an den sekundär befallenen Rüben (B); - Gesamtanzahl der Blätter; - Anzahl der befallenen Blätter; I-VII - Virginogene Generation.

(4) Veränderungen im Gesamtstickstoffinhalt und der Gesamtzuckerstoffe in den Zuckerrübenblättern; an der Achse X sind die Tage der chemischen Analysen, an der Achse Y der Inhalt des Gesamtstickstoffes und der Zuckerstoffe in % der Trockenmasse, rechts das Verhältnis der Gesamtzuckerstoffe: Gesamstickstoff. - Zuckerstoffe; - Stickstoff; - Veränderungen im Verhältnis der Gesamtzuckerstoffe: Gesamtstickstoff.

THE EFFECT OF VARIOUS SUBSTANCES ON THE DEVELOPMENT OF APHIDS

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Substances can be put into aphids in various ways, by injection, or by causing them to suck through membranes (4, 1). To give the aphids a certain amount of freedom and to influence their growth by a single substance, plants were used oversaturated with organic carbohydrates and compounds containing nitrogen (glucose and saccharose; glycine and ammonium nitrate). The solutions were applied at concentration 0·02 M because at 0·05 M the plants did not remain healthy. *Vicia fabae* L. and the aphid *Megoura viciae* Buckt. were used.

Two methods were used to oversaturate the plants: (1) so-called vacuum-infiltration, which was not continued because of many disadvantages; (2) cutting off the roots of the whole plant whilst submerged in the desired solution, to prevent the incision from coming into contact with the air. The second method was used because the plants remained fresh for many days and the aphids fed and multiplied more or less successfully.

The food composition in plants has been studied analytically: osmotic pressure by refractometry, sugars and free amino-acids by papei chromatography.

When using carbohydrates for oversaturating plants, the amino-acid content remained constant and was the same as in the control plants. Great differences occurred in the sugar content: with glucose there was a fourfold increase of saccharose and a threefold increase of glucose after 24 hours; fructose remained constant. Glucose and fructose remained at the same level during the whole experiment, saccharose gradually decreased. When using saccharose the relation between the sugars was reversed.

The second group of experiments concerned nitrogenous substances. When glycine was used for the oversaturation of plants a most intense increase of serine with glycine, was observed. An increase of arginine, alanine, valine, and a striking increase of an unknown unidentified substance occurred. This unidentified substance was a spot on the chromatogram between asparagine and serine with glycine.

The behaviour of aphids put on these plants is of great interest. Each experiment consisted of a group of 3 plants on which 10 very young parthenogenetic females were put immediately after oversaturation.

When a higher concentration (0·05 M) was used, the aphids soon left the plants and walked on the walls of the cage, with great mortality on the second and third days. With plants treated with glycine the females bore almost as many nymphs as on the control plants, but a much lower birthrate was observed on the plants with much glucose or saccharose.

When a lower concentration (0·02 M) was used,, very different results were obtained. From the very beginning the aphids fed willingly and the total deathrate decreased considerably. The aphids on the plants with glycine and ammonium nitrate bore a considerably smaller number of nymphs than those fed with glucose and saccharose. The nymphs on the plants with nitrogenous substances needed a longer time for development than those on the plants filled with carbohydrates. The females were mostly wingless but in experiments with glucose and saccharose a few winged forms occurred.

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(3) INSECT BEHAVIOUR IN RELATION TO THE CONDITION OF THE HOST

THE ROLE OF REJECTIVE STIMULI IN THE HOST SELECTION OF PHYTOPHAGOUS INSECTS

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Investigations carried out in recent years on the host selection of chewing phytophagous insects showed that the host range is determined on the one hand, by the more or less specific responses of some chemoreceptors to feeding stimulants; and, on the other, by the sensitivity of probably other receptors to feeding inhibitors. Relatively much work has been done to find out the specific plant substances evoking normal feeding responses; but considerably less is known about the role of feeding inhibitors. This was probably because for a long time inhibitory factors were regarded as having importance mainly in determining the host range in polyphagous insects, while the host selection in oligophagous species was considered to be governed chiefly by the botanical distribution of specific feeding stimulants.

To obtain further data concerning the botanical occurrence of feeding inhibitors in relation to a given insect species, experiments were carried out on the adults of *Tanymecus dilaticollis* Gyll., *Phyllobius oblongus* L., *Phytodecta fornicata* Brüggm. and *Cassida nebulosa* L. (Coleoptera), and on the larvae of *Pieris brassicae* L. (Lepidoptera), using the leaf disc test and the sandwich-test.

The results of these experiments and the data available in the literature allow us to draw the following conclusions: (1) There appears to be a close correlation between the degree of host specificity and the sensitivity to rejectants. (2) As oligophagy is connected with the specialization of the chemoreceptors to specific feeding stimulants, it can be concluded that the more the chemoreceptors are specialized to feeding stimulants the more they are sensitive to feeding inhibitors. (3) While only a restricted group of substances can act as feeding stimulants to a given oligophagous insect, many substances of very different molecular structure are able to inhibit feeding. This narrow "negative" specialization of chemoreceptors makes it possible to reduce or impede feeding of the oligophagous insects on their host plants by treating the leaves with inhibitors. This possibility of protecting plants against insects is worthy of much more interest.

Investigations carried out on the egg deposition behaviour of insects with a strong specialization of oviposition site (as with *Bruchus pisorum* L., *Acanthoscelides obtectus* Say and *Athalia rosae* L.), showed that oviposition can be inhibited by various substances. This indicates the presence of a two-way specialization of the chemoreceptors governing the oviposition, similar to the chemoreceptor mechanism found in the host selection of chewing phytophagous insects.

FEEDING BEHAVIOUR OF THE APHID *MYZUS PERSICAE* (SULZER) IN RELATION TO THE SUITABILITY OF HOST PLANTS

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This paper reports on some of the various responses to different feeding solutions shown by adult apterous *M. persicae*. The relative acceptability of different fluids, was compared using simple choice-chambers in which the aphids had equal access to two fluids via a membrane of stretched Parafilm "M". Sucrose solutions were markedly preferred to water. Sucrose solutions containing a mixture of 6 L amino acids (asparagine, leucine, lysine, methionine, threonine and valine, each at 0·1%) were considerably more acceptable than a solution of sucrose only. A solution of the 6 amino acids alone was not discriminated from water. Solutions containing 0·1% neutral red were less acceptable than those without this dye.

Some insight into the gustatory discrimination by *M. persicae* of these and other fluids was obtained by recording the duration of the *initial* probes made by the aphids on a membrane into the test liquids or on a solid substrate e.g. a celluloid test-tube. On the latter, or with *N* HCl behind the membrane, the typical duration of initial probes was brief ($<\frac{1}{4}$ min.); with air or water it was normal (i.e., as on a host plant, $\frac{1}{4}$ to $\frac{1}{2}$ min.); with a solution of the 6 amino acids in water it was only slightly longer; but, with a 20% sucrose solution it was considerably longer ($>$ 1 min.). With 20% sucrose solutions containing the 6 amino acids or all the constituents of a complex nutritionally adequate diet, the typical duration of initial probes was markedly extended ($>$ 4 min.).

Whether or not the aphids insert their stylets deeply into the test fluids during the initial probes or during subsequent insertions was judged either directly, or on the basis of the salivary sheaths found on the membranes.

During initial probes lasting longer than 4 minutes the majority of insertions into 20% sucrose were deep; a smaller proportion of such probes into the 6 amino acid-sucrose solution were deep, and only rarely were the stylets observed to protrude into the complex diet.

During a 24 hour period, a large number of deep insertions (approximately 50 per aphid) were made into water (with or without the 6 amino acids), about half as many into 20% sucrose (with or without the 6 amino acids) and very few indeed into the complex diet. Tests with a mixture of all 20 dietary amino acids or of the dietary salts, whether dissolved in water or in 20% sucrose, showed a reduction in the number of deep insertions. The dietary vitamins, on the other hand, did not have a marked effect on depth of insertion, in the presence or absence of sucrose.

These results, in addition to providing a behavioural basis for the seeking out and acceptance by aphids of plant sap contained in certain plant tissues, emphasize that the qualitative and quantitative differences in amino acids and sugars known to exist between resistant and susceptible plants, and between different developmental stages in one and the same plant, not only influence aphids in a nutritional manner (as reported in our other communication), but may also have a more immediate effect which is expressed in the relative acceptance of different species, varieties or developmental stages of plants.

For example, when, for varietal or seasonal reasons, the amino acid concentration of the phloem sap is low, aphids sampling it may be expected to withdraw their stylets and to seek out a more acceptable (i.e. a more nutritionally satisfactory) food supply, either in the same plant, another plant of the same species, or even another host species.

It is hypothesized that such behavioural responses as aphids exhibit towards different liquids in the artificial feeding situation enter as a factor which regulates the suitability of a plant as a host for an aphid.

PRELIMINARY INVESTIGATIONS ON THE PALATABILITY OF WILD AND CULTIVATED PLANTS FOR *SCHISTOCERCA GREGARIA* FORSK. (ORTHOPTERA)

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The experiments were performed in a constant temperature room at $32 \pm 0{\cdot}5$°C and $55 \pm 0{\cdot}5$% R.H. illuminated 12 hours daily. Quantities of 6-10 grs. of four plants were placed in the corners of a cage containing 25 pairs of hypogenetic *S. gregaria* starved for 24 hours. Plants consumed entirely after 24 hours were discarded. Partially ingested or rejected plants were tested separately on 3 pairs of *S. gregaria* starved for 48 hours. Weighed leaves were offered during 3 days; leaf residue and faeces of 4 days were collected. The dry weight of residual leaves and faeces was determined, and the percentage of food ingested by each individual in 3 days was calculated.

Results and discussion. A considerable number of plants from different communities have been tested for palatability and repellence, and the results have made it possible to group the plants as (1) palatable, (2) partially palatable, (3) scarcely accepted or unpalatable. Palatable plants include xerophytes such as *Arnebia linearfolia* D.C., *Salvia ceratophylla* L. and *Astragalus bersabensis* Eig. et Sam., and plants rich in essential oils like *Thymus*, *Rosmarinus*, *Origanum* and others such as *Peganum and Inula* having a rue-like scent.

Most of the Solanaceae tested contain toxic alkaloids, e.g. Stramonium in *Datura*, Anabasine in *Nicotiana glauca* and glaucin in *Glaucium.*

It becomes evident from groups 2 and 3 that the Desert Locust has a pronounced attitude of adaptation to different plants. Some of those have relatively low water content while others, such as *Quercus*, contain in addition to that a high level of tannin. *Myrtus* and *Eucalyptus* contain volatile oils as well as tannin. *Artemisia* and *Thuja* contain thujone, *Rhamnus alaternus* is rich in certain glucosides. *Withania somnifera* produces narcotic and anti-epileptic substances.

The leaves of *Calotropis procera* contain calotropin and calotropagenin, and the latex which is present in all parts of this plant yields cardiac and fish poison, Gigantin. *Robinia pseudacacia* contains robin-toxalbumine. Among the scarcely accepted plants are found the more or less halophytic xerophytes e.g. *Anabasis*, *Arthrocnemum*, *Bassia*, *Chenolea* and also other genera having tender leaves as *Cercis* and *Acacia.* It seems that most of the scarcely palatable plants tested act by means of chemical repellents.

Nerium oleander which was found to be rejected by the Desert Locust is also untouched by grazing animals. Its leaves contain oleandrin and nerin a cardiotonic heterocide which is also found in *Urginea maritima* Bak. Adult Desert Locust were found to nibble only the midrib of *Nerium* leaves, whereas they feed partially on *Urginea maritima* after its leaves have withered. A similar observation was made also for *Pancratium maritimum. Asphodelus microcarpus* is accepted readily when cut into pieces, whereas undamaged leaves connected to a water supply are rejected. Freshly cut *Euphorbia* from which latex exudes was found to be repellent, whereas the leaves of the undamaged plant were accepted readily.

The only species that remained completely untouched by the locusts even after seven to eight days of starvation was *Melia azederach.* One may thus conclude that this plant contains a strong phagorepellent for the Desert Locust.

Since the stalks of some of the scarcely accepted plants are readily eaten by the adult locust, it may well be that field observations could have produced the erroneous impression that they are palatable.

It should be noted that locusts in captivity behave differently than in free flight. Consequently, the unpalatable plants, in groups 2 and 3, will be neglected in the field. In captivity, however, the locusts are influenced by hunger stimulus.

FACTORS AFFECTING HOST PLANT ACCEPTANCE IN SOME COLEOPTERA

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Any study of host plant selection in insects carried out to some extent, has shown that a chain of behaviour elements is involved, each of which is released or directed by its proper stimuli (2, 8, 7). In 1958, we have presented a provisional scheme of the sequence of stimuli and activities leading to host finding and acceptance by the larva of *Leptinotarsa decemlineata* (15). In this scheme, next to stimuli releasing or directing feeding responses or locomotory activities, stimuli occurred related to rejection of plants at different levels. Already in the paper by Chin (2) it was shown that palpectomised larvae may bite frequently in leaves normally rejected, such as *Doronicum*. A similar removal of inhibitory effects is produced by maxillectomy in the tobacco hornworm, *Protoparce sexta* (14).

On the level where the feeding action has started, resistance is produced in several solanaceous plants by substances such as Tomatin, Demissin, Leptin (6, 10). These substances of which the action on the tarsal chemoreceptons of the adult beetle has been shown beyond doubt (11), were designated by us as "rejectants", but may now be referred to as "feeding deterrents" (3).

Host plant selection in the adult Colorado beetle has been studied much more fragmentarily than in the larva, but fiom previous work (5, 9, 11, 12) and from some of our own experiments it follows that it occurs in many respects along the same lines, at least as far as olfactory and gustatory stimuli are concerned.

In this paper, we intend to compare host selection in the leaf-eating Colorado beetle with that in the fruit boring Coffee berry beetle (*Stephanoderes hampei* Ferr.) and in the Coffee Ambrosia beetle (*Xyleborus compactus* Eichh.). Work on these Scolytids has been recently carried out in the Ivory Coast (1, 13).

Most of the experiments were made with a quantified version of Dethier's screen test (3). The substance to be tested was placed in one half of a Petri dish cover, over which nylon or copper gauze of fine mesh was stretched. The other half was either left empty or filled with reference substances. To test optical effects, the material was covered by both cellophane and gauze. The females to be tested were placed in the centre. Their distribution above the two halves was checked after 5 minutes. The experiment was repeated ten times. The deviation from 50% distribution was calculated and its transgression probability. The results are considered significant if $P \leqslant 0{\cdot}05$.

Fruit Selection by *Stephanoderes*.

The young female of *Stephanoderes* is fertilised while still in the fruit. It subsequently leaves the fruit at about mid-day and performs its infection flight, lasting from some minutes to a few hours. Many females search for fruits in the immediate vicinity. These fruits may range in maturity from green to black. It was shown that black and red berries are preferred.

In one experiment the preference order of red, yellow and green berries was 61, 29 and 10%. "Artificial berries" confected from stained cotton wool balls covered with paraffin, were easily penetrated by the beetles. Black, red, green and yellow balls were preferred in that order. It was subsequently found that in a "screen test" both red and green berries were preferred to dry and moist filter paper.

Covering with cellophane removed the attractiveness of the berries in this test.

From the fact that beetles penetrate into paraffin covered cotton balls, it follows that most probably the tactile properties of the fruit are of importance.

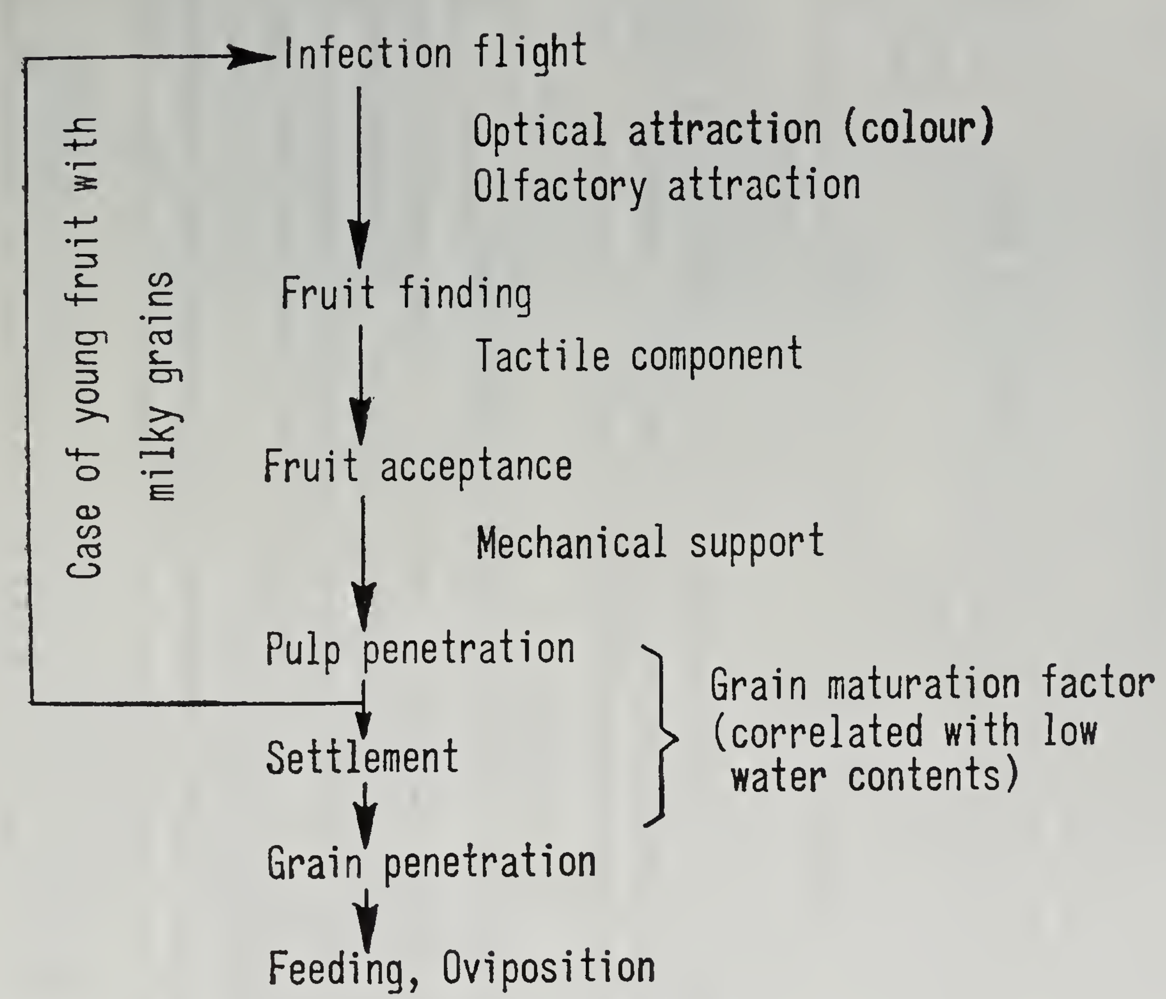
Penetration into the pulp requires a support, either given by the crown of attacked berries or, in case these have dropped from the tree, by the soil.

Subsequent penetration into the grain requires a "maturity factor". Young, milky grains are never penetrated. The female either leaves the berry or waits until maturation.

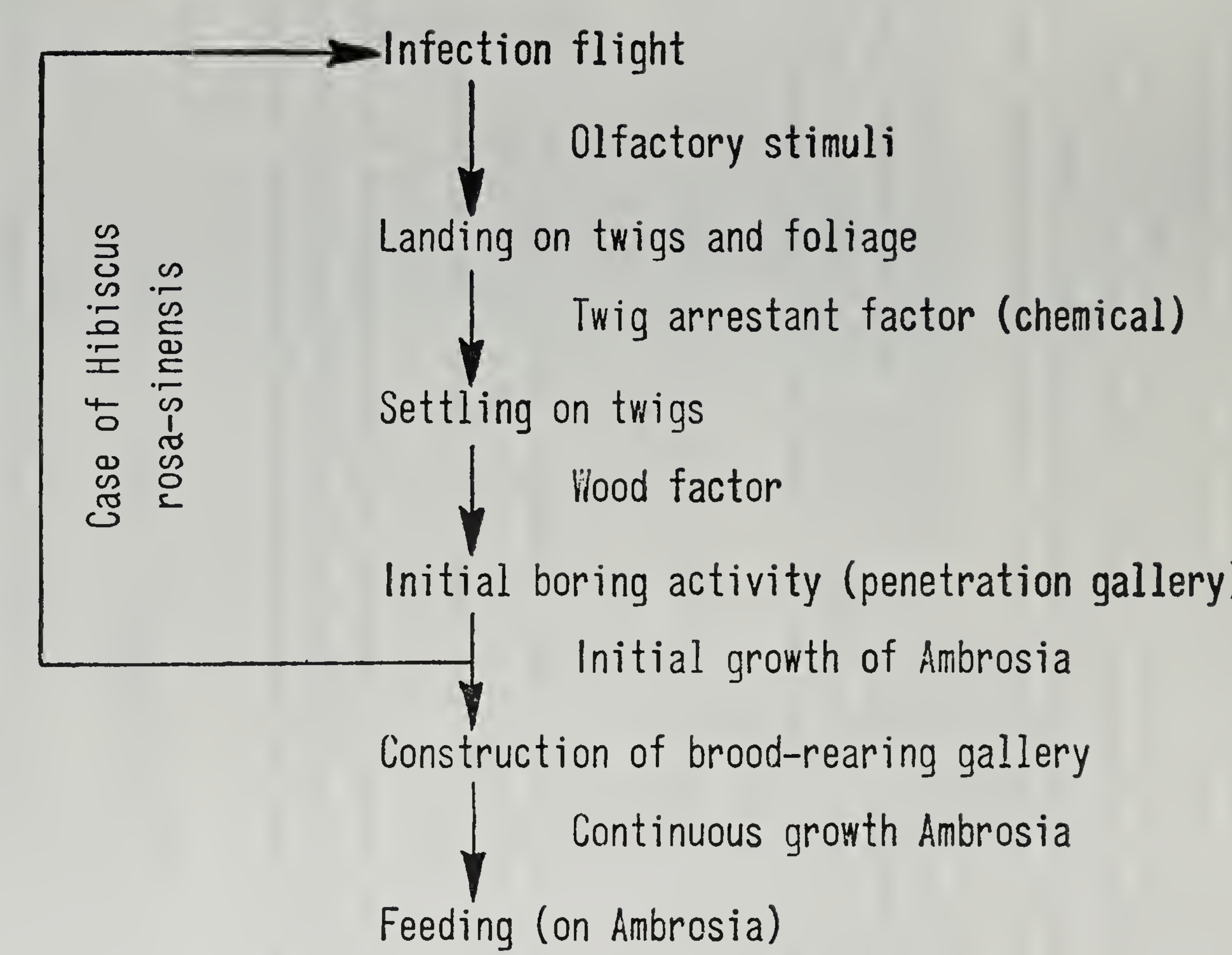
The above steps in host selection of *Stephanoderes* are summarised in fig. 1.

Twig Selection for Breeding in *Xyleborus compactus* Eichh.

Xyleborus compactus feeds exclusively on a fungus, *Ambrosiella xylebori* Brader, which it transfers into the branches of several trees. Coffee is most frequently infested. The young



1. **Provisional** scheme of host selection in Stephanoderes hampeĩ, Ferr



2. Provisional scheme of host selection in Xyleborus compactus Eichh.

(= X. morstatti Hag.).

FIG. 1. Provisional scheme of fruit selection in the female coffee berry borer, *Stephanoderes hampei* Ferr. (after the data from Tischler, 1961).

FIG. 2. Provisional scheme of host plant selection in the female coffee twig borer, *Xyleborus compactus* Eichh. (after the data from Brader, 1964).

female is fertilised in the gallery in which it has been born. Like *Stephanoderes*, it leaves the gallery after maturation at about mid-day. Dispersion flights may be extensive, but frequently the female bores a new hole in the near vicinity of the mother-gallery. As judged by the screen test, the smell of coffee twigs and leaves is attractive to *Xyleborus*, and *C. robusta* is preferred to *C. liberica*. Leaves of *robusta* are more attractive than twigs.

The attractiveness of *robusta* twigs is partly explained by the observation made in the screen-test, that the number of beetles taking flight is much reduced above *robusta* twigs. These twigs most probably contain an "arrestant" (4).

The female subsequently bores a penetration gallery. The bark of the twig is insignificant in attraction, as the female bores more readily in twigs from which the bark had been stripped. It seems that the xylem contains most of the attractive factor. While in the xylem, the female disseminates its fungus, the initial growth of which seems to be awaited. When it occurs, the breeding gallery is constructed in the central marrow.

In *Hibiscus rosa-sinensis*, in which the fungus does not grow, gallery boring is never completed but always stopped at the xylem-stage (fig. 2).

Role of the Antennae.

In *Lepinotarsa*, olfactory responses to the host plant disappear after antennectomy (9). The same is true for *Xyleborus compactus*.

However, in *Stephanoderes* the responses in the screen-test persist after antennectomy suggesting a role of the palpi.

Though the three species mentioned above, represent very different types of host plant relations, it is clear that host specificity is determined by a sequential process, in which stimuli of various nature are involved. Initial attractiveness of a plant is not necessarily correlated with final acceptibility.

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INFLUENCE DE LA PLANTE-HOTE SUR L'ACTIVITE REPRODUCTRICE DE LA TEIGNE DE LA BETTERAVE *SCROBIPALPA* (*PHTHORIMAEA*) *OCELLATELLA* BOYD (LEPIDOPTERE PLUTELLIDAE)

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L'analyse des facteurs conditionnant l'activité de ponte d'un Lépidoptère phytophage, la Teigne de la Betterave *Scrobipalpa ocellatella* a permis de montrer une action stimulatrice de la plante-hôte sur l'activité ovarienne. En s'adressant à un insecte dont les adultes ne s'alimentent pas au dépens du végétal pendant la ponte, l'influence des stimulations chimiques de la plante a pû être dissociée de l'influence alimentaire.

Les insectes sont récoltés dans les champs au stade de chenilles adultes qui se nymphosent au laboratoire. Les expériences sont conduites dans des conditions de milieu bien définies toujours identiques.

I.—la ponte

Le comportement de ponte de la Teigne de la Betterave est sous la dépendance de deux

facteurs: (*a*) un facteur chimique spécifique à la Betterave, soluble dans l'eau et l'alcool éthylique, (*b*) un facteur tactile représenté par la rugosité du support. Ces deux stimuli interviennent dans la localisation des oeufs et ont une influence sur l'intensité de la ponte.

(1) *Localisation des oeufs.* Des femelles groupées sont élevées en présence de différents supports présentés simultanément et portant les stimuli tactile et chimique associés ou non (tableau).

Pourcentage des oeufs pondus sur divers supports

	Supports avec *Stimulus chimique + rugosité*	*Stimulus chimique seul*	*Stimulus rugosité seul*	*Supports nus*	*Parois cage*
Expérience 1	78%	0%	20%	0%	2%
Expérience 2		12%	80%		8%
Expérience 3		72%		11%	17%

Le facteur tactile apparaît comme très important dans le choix du lieu de ponte (expérience 1 et 2) et semble jouer un rôle plus grand que chez *Plutella maculipennis* Curt. (1). Le facteur chimique isolé est choisi lorsque la rugosité est absente (expérience 3). Ces mécanismes de localisation des oeufs assurent des conditions favorables à la prise d'alimentation des jeunes larves.

(2) *Intensité de la ponte.* Des femelles sont élevées isolément pendant toute leur vie en présence d'un seul des supports utilisés dans les expériences précédentes.

(*a*) en absence des facteurs chimique et tactile, la moitié des mères ne pondent pas. Les autres sont peu fertiles et déposent en moyenne chacune 68 oeufs.

(*b*) en présence du facteur rugosité seul, 93% des femelles sont fertiles et déposent en moyenne 110 oeufs.

(*c*) en présence du facteur chimique seul, 93% des mères sont fertiles et déposent en moyenne 161 oeufs.

(*d*) l'association des deux facteurs induit le comportement de ponte chez toutes les femelles qui ont une fécondité moyenne de 208 oeufs. Dans ce dernier cas, l'activité reproductrice est comparable à celle des femelles pourvues en Betterave.

La fécondité dépend de la nature des facteurs présentés. Le stimulus rugosité seul déclenche le comportement de ponte mais la quantité d'oeufs est faible. Au contraire, le stimulus chimique spécifique et l'association des 2 stimuli entraînent une grande activité reproductrice. La plus grande masse des oeufs n'est expulsée que lorsque les femelles rencontrent un ensemble de stimulations liées avec la plante-hôte, c'est-à-dire des conditions assurant la survie de la descendance.

II.—INFLUENCE DE LA PLANTE SUR L'ACTIVITE OVARIENNE

A l'émergence des papillons, l'ovogenèse et la maturation des oeufs sont rapides; le 2e jour, 60 à 80 oeufs sont stockés à l'intérieur du système génital. Le devenir de ces oeufs mûrs a été suivi par dissection chez des femelles vierges qui ne présentent jamais d'activité de ponte. *Le stock d'oeufs reste invariable chez les femelles en contact avec un plant de Betterave ou avec un extrait de la plante. Au contraire, l'absence de la plante-hôte entraine rapidement la resorption des oeufs mûrs stockés.*

Dans le champ de Betteraves, les femelles vierges peuvent pondre très vite quand un mâle est rencontré même au bout de 18 jours. Chez les mères fécondées ou non, éloignées des cultures de Betteraves, les oeufs régressent et la longévité est accrue. La résorption des oeufs n'entraine pas la stérilité, une nouvelle ovogenèse reste possible lors d'une rencontre même tardive avec la plante. Ainsi, les mères gardent le pouvoir de se reproduire si la plante-hôte fait défaut pendant une période pouvant dépasser 3 semaines.

Il est montré que l'hôte exerce, en-dehors de toute intervention alimentaire, une action stimulatrice spécifique de nature chimique sur l'activité ovarienne. Labeyrie (2, 3) a décrit des actions du même ordre chez deux autres insectes.

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CHEMICAL PHAGOSTIMULATION IN *EPILACHNA FULVOSIGNATA* (COLEOPTERA, COCCINELLIDAE)

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The Epilachninae is a group of leaf eating lady beetles particularly well suited for the study of problems associated with the chemical basis of host plant selection by insects. Many species of *Epilachna* are associated either with the Solanaceae or Cucurbitaceae, and *Epilachna fulvosignata* occurs frequently on *Solanum campylacanthum* in Uganda. The presence of two larval phagostimulants in this plant has been demonstrated. One is steam volatile and the other not so.

In order to detect the presence of phagostimulatory substances the materials to be tested were incorporated in agar solutions which were then poured and allowed to set in petri dishes. When set the agar gels were inverted, so that the smooth sides lay uppermost, and discs were cut from them with a cork borer. To compare the properties of two agars, two discs from each agar were placed in each of ten petri dishes (lined with damp filter papers) and the larvae added. After some 14-18 hours the dishes were examined and the agar discs scored on an arbitrary scale according to the area of surface damaged by the larvae. Initially such comparisons were made between 41 pairs of identical agars. An idea of the differences likely to arise from experimental errors was obtained by plotting the lowest score of each pair against the difference in score of that pair. In subsequent work two comparisons (each involving 10 dishes) were made of the agars concerned. If, in both comparisons, the differences were greater than the expected experimental error, they were attributed to genuine differences in phagostimulation.

Oil containing the volatile phagostimulant was prepared as follows. On successive days 8 kg lots of fresh *Solanum* leaves were deep frozen for 24 hours, extracted with 16 litres water for another 24 hours, expressed through cloth, and the filtrate steam distilled. The first 500 ml distillate were collected and stored in the refrigerator. When some four or five distillates had been obtained from successive batches of leaves they were bulked and distilled gently through a Vigreux column. The column temperature was raised slowly and the head maintained at 90°C for about half an hour before steam was allowed to pass over into the distillate. The distillate was redistilled in a Claisen flask, and the temperature maintained between 75°C 80°C until distillation ceased. A small drop of oil containing the phagostimulant separated out from the water in the distillation flask. It was extracted with ether.

This oil can be detected by the larvae in concentrations down to 2 p.p.m. agar solution. It is 95% one component but it is uncertain whether this major component is the phagostimulant. Only 0·3-0·5 ml oil have been obtained from 100 kg fresh leaves. The further-fractionation of this oil and the identification of the phagostimulant has been undertaken by Dr. R. D. M. Murray of the Chemistry Department of Glasgow University.

PERSISTENCE AND USES OF SOIL INSECTICIDES

PERSISTENCE AND BEHAVIOUR OF PESTICIDAL RESIDUES IN SOILS AND THEIR TRANSLOCATION INTO CROPS

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The amounts of synthetic chemicals, including various kinds of pesticides, produced during the last 20 years are relatively large. Various problems have been encountered with organic insecticides of which some were found to be more persistent than originally anticipated. It is, therefore, necessary to find out if, and to what an extent, pesticidal residues might have an effect on humans, animal life, soils and plants grown therein.

Soils are being contaminated either through "fall out" after crop spraying for insect control or due to direct soil treatment with insecticides. The persistence or breakdown of insecticidal chemicals in soils depends on various factors:

(1) *The insecticide itself.* Insecticides of the chlorinated hydrocarbon group such as DDT, aldrin and heptachlor are more persistent than those of the organophosphorus group. Large differences also exist within each group of chemicals whose half lives in soil range from several months to days. After an application of parathion, methylparathion and malathion at 5 lbs./acre to loam plots, residue levels of 0·1 p.p.m. (3% of the applied dosage) were reached under field conditions with malathion within 8 days, with methylparathion within 30 days and with parathion within 90 days.

(2) *Soil type.* Insecticides persist longer in soils of high organic matter than in those of low organic matter content. In a muck soil (organic matter approximately 50%) insecticidal residues are bound to the soil particles to such an extent that the same amount of toxicant is less effective in a muck soil as compared to a sandy one.

(3) *Moisture.* Moisture enhances the release of volatile insecticides from soil particles, and also influences the breakdown of other insecticides by way of hydrolysis. In addition attacks of microorganisms on insecticidal chemicals require certain moisture conditions. While one of the main reasons for the loss of aldrin or heptachlor residues from soil was found to be volatilization of the chemical, parathion is detoxified and disappears through hydrolysis or reduction to its aminoform.

(4) *Microorganisms* in soil attack various insecticides. In dry or autoclaved soils, both aldrin and parathion persist longer than in wet and non-autoclaved soils. Due to microbiological activities aldrin is oxidized to dieldrin, while parathion, in the presence of yeast, is reduced to the non-toxic aminoparathion.

(5) *Soil temperatures* have a remarkable effect on the rate of loss of an insecticide. They influence both the loss through volatilization as well as the break down of the insecticide by biological and chemical factors.

(6) *Cover crops*, such as alfalfa, in insecticide treated fields increase the persistence of volatile pesticides in soils.

(7) *Cultivating of soils* increases the disappearance of insecticidal residues from soils. Under field conditions, daily disking of a loam soil treated with aldrin or DDT at 4 lbs./5″ acre caused a reduction of 38% of the aldrin residues and 25% of the DDT residues, during a 3-month period.

(8) *The mode of insecticidal application and the formulation* used are decisive factors in the persistence of insecticidal residues in soils. The greatest loss of aldrin residues occurred in soils where the insecticide was left on the soil surface following an emulsion application. The greatest persistence of residues was noticed after granules had been incorporated into the upper 4-5 inch soil layer.

RESIDUE LEVELS AFTER REPEATED ANNUAL SOIL TREATMENTS

Applications of three yearly dosages of one pound per 5″ acre (loam soil) of aldrin or heptachlor resulted in residue levels of 0·6 pounds per acre (20% of the totally applied dosage) at the end of the three-year period. Applications of five yearly dosages of 5 pounds per 5″ acre

of aldrin or heptachlor resulted in residue levels of 4·6 pounds per acre (18% of the totally applied dosage) at the end of the five year period. Application of one massive dosage of 25 pounds per 5″ acre of either aldrin or heptachlor resulted five years later in residue levels amounting to only 10% of the applied dosage.

Translocation of some chlorinated hydrocarbon insecticides from soils into the edible parts of crops occurs to various degrees. Some crops do not absorb any insecticidal residues, while others translocate the chemicals at various amounts. Potatoes, radishes and carrots, grown on a loam soil treated with aldrin at one pound per acre contained residues at concentrations of zero, 0·03 and 0·05 p.p.m. respectively. Carrots absorbed more residues than any other crop. Considerable differences in the rate of absorption of aldrin and heptachlor residues by five carrot varieties were noticed. The concentration of translocated chemicals in the carrots varied from 22 to 80% of the insecticidal concentration in the soil. No correlation could be established between the amounts of ether-extractable substances within the five carrot varieties and the ability of the carrot tissue to absorb, or store, insecticidal residues.

All field data were obtained under Wisconsin conditions: average yearly rainfall of 30·16 inches or 766 millimeter, average yearly temperature of 45·3°F or 7·3°C, average temperature for the period May through October, 62·4°F or 16·9°C.

THE PERSISTENCE, ACCUMULATION AND BEHAVIOUR OF ORGANOCHLORINE INSECTICIDES IN SOIL

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The principal organochlorine insecticides used in agriculture in the U.K. have been lindane, aldrin, dieldrin and DDT and a high proportion of arable fields are believed to contain residues of these compounds (6). Lindane used as a seed-dressing does not give rise to any residue problems. Although aldrin itself is slightly less persistent in soil than lindane, it has been used more extensively and in larger amounts and its application leads inevitably by epoxidation to residues of dieldrin in the soil. Many arable soils may now contain residues of 0·2 to 0·5 ppm of dieldrin and, where aldrin or dieldrin have been most intensively used, residues of up to 1 ppm or more may not be uncommon (1). DDT residues of up to about 2 ppm also occur in some arable soils and many soils now contain small residues of DDT, which tends to be even more persistent than dieldrin.

In an experiment started at Wellesbourne in 1956, 1, 2 and 3 lb. dieldrin per acre was mixed into a sandy loam soil and the residues were assayed from 3·5 to 7·8 years after treatment. Although the average rate of loss during this period was only 7-8 per cent per annum, it was evident that the rate of loss initially had been much greater. The results of a similar experiment done on organic fen soil at Mepal, Cambridgeshire also indicated a high initial loss. In contrast, no rapid initial loss occurred at Wellesbourne when dieldrin in amounts ranging from 0·05 to 1·25 lb per acre was mixed into soil and no measureable decline in residues has been recorded 58 and 85 weeks after application.

Undisturbed residues of dieldrin on the soil surface, however, have been found to be lost much more quickly, only 8-10 weeks being required for half of the applied amounts to disappear during the summer months (7). Similar results have been obtained in the U.S.A. with aldrin and heptachlor (3). Owing to the difficulty of finding dieldrin and DDT-free sites for field experiments, microplots have been used for certain types of studies. The results obtained from microplots appear to be comparable with those from orthodox field experiments.

Residues can only accumulate in soils if the amounts used exceed the amounts lost in the intervals between applications, so accumulation is essentially a predictable phenomenon. If the amounts of insecticide applied and the frequency of application are known, and the average

rates of loss can be estimated, reasonable predictions of any likely accumulation can be made (5). Theoretically, a residue should not increase indefinitely but should tend towards a maximum when the amounts lost between applications equals the amount applied on each occasion. For example, assuming the rate of loss to be exponential, unit amounts applied at intervals of $\frac{1}{2}$, 1 or 2 "half-life" periods would lead in the *n*th cycle of events to maxima of 3·4, 2 or 1·3 units of residue respectively. The limit should be reached after a few cycles, but, since in practice a cycle may occupy several years, this thesis cannot be readily demonstrated experimentally with very persistent insecticides.

Slight downward movements of DDT, lindane and aldrin from the cultivated layer of soil have been observed when large amounts have been applied (2), but even 4 years after treatment, only minute traces of dieldrin have been found below the cultivated layer in the U.K. (4). A microplot experiment has shown that dieldrin located initially in very thin layers at depths of 2·5, 10 or 25 cm remained mainly within 1 to 1·5 cm of the original position 6 months after application. Since the errors of sampling soil at precisely defined depths must be of this order, it was concluded that passive movement during this period was very limited. The persistence of the dieldrin was similar at all three depths, and carrots grown in these plots had the highest residues in the peel adjacent to the treated layers of soil. Even when the dieldrin was placed 25 cm deep, appreciable residues were found in carrot peel although the maximum depth reached by the swollen part of the roots was only 20 cm and the mean depth 12 cm. Surprisingly, dieldrin at this depth also controlled carrot fly (*Psila rosae* (F.)) better than when at 2·5 cm, although the most effective depth appeared to be 10 cm, and it is evident that residues in at least the upper 25 cm of soil must be considered biologically important.

Low concentrations (0·05-0·4 ppm) of dieldrin very intimately mixed with soil can control carrot fly and periodic cultivations may very well improve the efficiency of ageing residues. However, at very low concentrations the carrot fly larvae tend to feed for a while before dying but the lesions formed can heal leaving only some atypical damage apparent on the carrots.

If a residue in soil declines exponentially with time, the proportion p remaining at time t is given by $p = e^{-kt}$ where k is a constant, and log p would be a linear function of time. It is obvious from studies already done that the loss of insecticides from soil does not fit this simple model. This is not surprising considering the known complexity of mechanisms contributing simultaneously to the loss of an insecticide under varying conditions. The study since 1955 of a DDT residue in a field plot at Wellesbourne indicates that the "half-life" value itself has changed gradually from about 2·5 years in the first year to about 25 years by the ninth year after treatment, and the logarithm of the "half-life" indicated from year to year was apparently linearly related to time. This finding has led a colleague, Mr. J. A. Nelder, to suggest an alternative model in which the residue is imagined as existing in a population of sites each having an individual loss rate k. The choice of an appropriate frequency distribution for k has given the relationship $p^{-\theta} = 1 + ct$ where θ is the measure of the diversity or spread of k and c/θ is a measure of the *mean* loss rate k. The model appears to be logical and families of curves can be derived which resemble closely the types of decay curves found in experiments, both the high initial loss phase and the slow subsequent changes being accounted for. Studies of the values of the parameters θ and c are in progress in the hope that they will lead to a fuller understanding of the rates of loss of insecticide residues from soil.

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THE ACCUMULATION AND DISSIPATION OF RESIDUES RESULTING FROM THE USE OF ALDRIN IN SOILS

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Aldrin, when properly applied and incorporated in the soil, effectively controls most of the subterranean insects that attack the roots of corn in Illinois. For this and other reasons, aldrin soil treatments, introduced experimentally in 1950, have increased until Illinois farmers now treat 3 to 4 million acres each year. The value of these treatments in increased production and income, as estimated by Illinois farm advisers, ranges from 15 to 25 million dollars per year over and above the cost of the treatment.

A number of studies conducted in Illinois, elsewhere in the United States and abroad, clearly indicate that residues resulting from applications of aldrin on growing plants or used as a soil treatment diminish very rapidly during the first few days or months, and continue to decline thereafter.

In dozens of tests conducted over a period of 10 years, whenever aldrin was applied to typical Illinois corn belt soils and worked into the ground as recommended, two typical phenomena became clearly evident within a few weeks or months: A portion of the aldrin (15-30%) was converted to dieldrin and an even larger portion was lost through evaporation. Under the conditions that prevailed in central Illinois in early May and June, 1958, with mean temperatures ranging from 58° to 75°F, 30 days after application the total of aldrin and dieldrin (0·21 ppm) was less than 1/3 of the amount of chemical applied (0·75 ppm) and nearly 20% of it (0·04 ppm) was dieldrin. Within 60 to 120 days, dieldrin residues reached their peak (0·085 to 0·125) which was only about 10 to 15% of the amount of aldrin applied.

The following spring, approximately one year after the aldrin was applied, the aldrin residues had dropped to between 0·012 and 0·019 ppm and the dieldrin residue had declined about 1/3 to between 0·075 and 0·106 ppm. The total aldrin + dieldrin residue at this point was only about 10 to 15% of the amount applied.

When the residues (aldrin + dieldrin) found at yearly intervals after single applications of aldrin are plotted against time (in years), it becomes apparent that residues decline rapidly so long as aldrin predominates, but once the residues are predominantly dieldrin, the rate of loss assumes the characteristic of a first-order reaction and is reduced by 50% each 2 to 4 years, depending upon a number of variables such as temperature, moisture, and degree of tillage. An inspection of graphs of this type suggests several generalizations: (1) residues should not be greater than 20% of the amount applied at the end of the second year, and reduced by 17·5% each year thereafter; (2) approximate residue for any given year would be 15% of the amount applied at the end of the second year and reduced by 20% each year thereafter; and (3) the residue should not be less than 10% of the amount applied at the end of the second year and reduced by 30% each year thereafter.

Assuming a 4-year half life for dieldrin from the second year on, one envisages accumulated residues after 10 years, perhaps amounting to 125·5% of the annual application rate, and if annual applications were continued for 25 years, this could go on up to 150% or 1½ times the rate of application.

On the other hand, for fields under intensive cultivation, assuming a half life of 2 years after the second year, annual applications for a period of 10 years would produce a total accumulation of aldrin plus dieldrin of only 91% of the annual application rate. From this point on, additions are so small they would be only 94% in 20 years and 95% in 25 years. Thus for practical purposes one might assume that under such conditions residues have reached a point where annual losses would equal the annual additions and accumulated residues greater than the equivalent of one year's application rate would not be expected.

To test the validity of these hypotheses and the generalizations suggested earlier, soil samples were collected from 35 Illinois corn fields having known histories of aldrin treatment. These were analysed to determine the actual residues present in the spring of 1963 and the results compared with the theoretical values developed by the several hypothetical formulae.

Utilizing values wherein average conditions presume a dieldrin half life of 4 years, the ratios (actual over theoretical) ranged from 44 to 99 and averaged 69. It would appear,

therefore, that since in all of the 35 fields studied the theoretical values were in excess of the actual residues found, the generalized assumption that a 4-year half life for dieldrin would cover the maximum values expected, was correct.

Even more significant, in only one of the 35 fields did the actual residue exceed the annual rate of application (105%). Even here the actual residue appears high, indicating the possibility of an error in application, sampling or analysis. It is worthy of note that even though: (1) rates of application varied from $\frac{3}{4}$ to 3 pounds per acre, (2) the number of annual applications ranged as high as 13, and (3) the total amount applied varied from 4 to 30 pounds per acre, the residues found one year after the last application averaged only 8·85% and never exceeded 13·2% of the total amount applied.

While all the data presented herein were obtained under conditions prevailing in Illinois, it appears the findings have a much broader application. Data obtained in England by Wheatley *et al.* (1962) are in substantial agreement with the Illinois data. Likewise, the concept posed here fits the data from British Columbia, Canada, presented by Wilkinson *et al.* (1964). They reported dieldrin residues of 0·098 and 0·153 ppm nine years after an application of aldrin at the rate of 2·5 ppm, and on the basis of 20% at the end of the second yeaı and a 4-year half life thereafter we would anticipate a residue of 0·15 which is 6% of the amount applied.

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THE PERSISTENCE OF SOME INSECTICIDES IN SOIL AND THEIR EFFECTS ON SOIL ANIMALS

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Small plots on newly-ploughed old pasture with silt loam soil were sprayed with DDT at 6, 15 and 60 lbs. a.i. or aldrin at 4 lbs. a.i. per acre, then double-rotovated six inches deep. Plots which were three metres square were replicated four times with four controls and kept fallow. Sixteen 2″ diam. and seventy-two 1″ diam. cores, all 6″ deep, were taken from each treatment every two months. The 1″ diam. samples from each plot were bulked, thoroughly mixed and subsampled twice. One subsample was placed in a Baerman funnel (2) and nematodes extracted. Insecticides were extracted from another subsample by tumbling with acetone and hexane for 3 hours, then removing the acetone with 2% sodium sulphate solution. Extract aliquots were analysed by gas-liquid chromatography on a column composed of 2·5% silicone elastomer E 301 and 0·25% epikote 1001 on celite (3), with detection by electron capture.

Fig. 1 gives average residues of aldrin; after 39 months most aldrin had disappeared, the active insecticidal residue was 40% of that applied but nearly all dieldrin. Insecticide was lost rapidly for four months, then more gradually; about half the original dose had disappeared after four months; rather less than found by Lichtenstein (5) but much more than estimates by Wheatley (7) who gave a "half-life" of aldrin as 3-4 years.

Fig. 2 summarizes DDT disappearance. After 39 months 77% remained in plots treated with 60 lbs. a.i. and 73% in those with 6 lbs. a.i. per acre; this agreed with regressions calculated from all available data which showed that smaller doses disappeared proportionally faster than large (1). The main breakdown intermediary was relatively transient DDE.

Soil animals were extracted from the 2″ diam. samples, either by Salt and Hollick flotation (6), or in Tullgren funnels (4).

DDT and aldrin affected soil animal numbers very differently. Aldrin (or converted dieldrin) did not change numbers of predatory mites, but killed most other soil mites; most species of Collembola were greatly reduced in numbers by aldrin; the larger and more active surface-dwelling species were most affected. Symphylids, pauropods, root aphids and caterpillars were only slightly affected by aldrin in soil, but almost all dipterous and coleopterous

larvae were killed. Numbers of nematodes, enchytraeid worms and earthworms were unchanged.

DDT was generally less lethal to soil animals than aldrin, but killed a large proportion of predatory mites, and the larger doses also killed saprophagous mites. At all doses there were increased numbers of Collembola in DDT-treated soil; there seems little doubt that the increase is due to lower numbers of predatory mites. Fewer dipterous or coleopterous larvae were killed by DDT than by aldrin, except at the largest dose; more symphylids, pauropods, root aphids and caterpillars were killed by DDT than by aldrin. Numbers of nematodes, enchytraeid worms and earthworms were unaffected by DDT.

The effects of the insecticides were not devastating; no serious side-effects were apparent.

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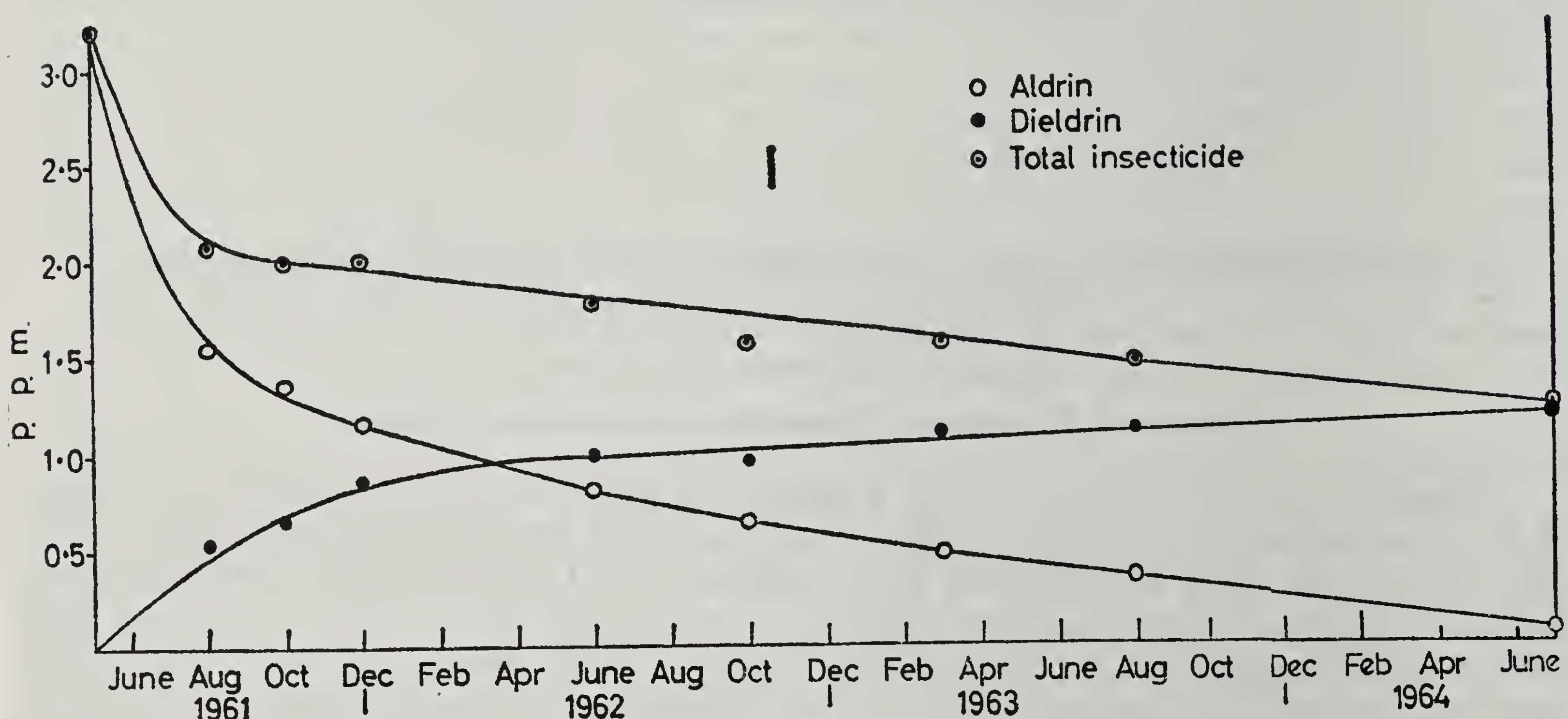

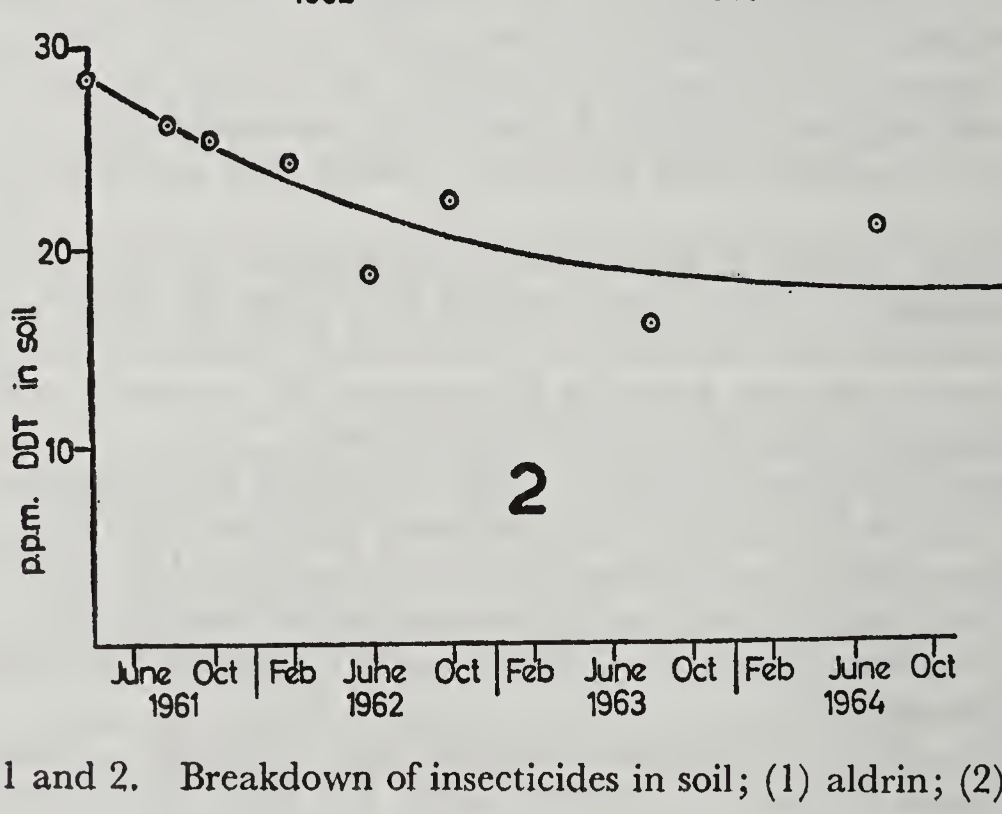

Figs. 1 and 2. Breakdown of insecticides in soil; (1) aldrin; (2) D.D.T.

SEEDLING EMERGENCE AFFECTED BY SOIL APPLICATIONS OF INSECTICIDES

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The versatility of systemic insecticides for soil application was immeasurably broadened by the development of the granular formulation. The chemically charged granules may be sown in the row with the seeds where they come into intimate contact with the roots of the seedlings. This ensures an immediate uptake of toxicant which protects the emerging seedling from insect attack at a very vulnerable stage of growth. Evidence indicates that a localized placement of systemic chemicals is more effective than a broadcast application mixed thoroughly with the soil.

Systemic insecticides applied at planting time with lettuce seeds are as effective as foliar sprays for protection of the crop from feeding by leafhopper, *Macrosteles fascifrons*, a vector of aster yellows virus. This disease is often serious, necessitating an exacting spraying schedule to control the leafhopper and thereby reduce spread of the virus. Effective systemics properly applied in the row with the seeds will eliminate the necessity of spray applications.

However, stands are reduced and in some instances near failures have resulted from systemic insecticide applications. Experiments were conducted in the greenhouse to determine the causes of the failures. Organic soil was used in the trials since commercial plantings of lettuce are grown almost exclusively on the mucklands or fens in New York State.

The reason for the marked decrease in stand is attributed not to phytotoxicity but to an increased infection by soil organisms causing damping-off. Both pre-emergence and post-emergence infection is significantly increased with the use of in-row application of phorate and Di Syston.

This adverse effect appears to be characteristic of the organophosphate compounds. Although investigations have not been extensive to date some carbamate compounds also depress stands. The organochlorine insecticides have no pronounced effect upon seedling emergence but post-emergence infection is greater than in the controls.

Reasons for the increased infection appear to be two fold. First there is a delay in sprouting in treated rows which allows for a longer period during which the seedlings are most susceptible to infection. Lettuce seeds were most vulnerable to infection by seed rotting pathogens during the first 24 hours of incubation at 70°F. in the laboratory. When phorate was applied with the seed a delay in seedling emergence of 2 to 3 days occurred with a resultant loss of stand. Retardation in seedling emergence was less with Di Syston and infection was also lower.

A second possibility contributing to increased infection is the effect of the systemic chemicals on the non-pathogenic organisms that compete with the pathogens. Growth and activity of the pathogens are inhibited by the competition, a condition known as fungistasis. Plating of the organic soil in the usual mannei to determine populations of soil bacteria and fungi indicated a depressed count of bacterial colonies at high concentrations of phorate but fungal growths were approximately normal. The suggestion is offered that phorate, the only chemical investigated at this point, reduces the bacterial activity associated with the rhizospheres of the roots and thereby allows fungi, such as *Pythium* and *Rhizoctonia*, a less impeded contact with the roots.

Judicious use of fungicides protected the seedlings from infection. Thiram (tetramethylthiruram disulphide), captan (N-trichloro Methylmercapto-4-cyclohexene-1,2 dicarboximide) and Dexon (p-Dimethylaminobenzenediazo sodium sulfonate) were effective in reducing seed decay and damping-off. A comparison of seed dressings with granule dressings showed a significant improvement in control of infection with the former.

ÖKOLOGIE UND BEKÄMPFUNG DER DRAHTWÜRMER IN DER UKRAINE

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In der Ukraine sind 23 Schädlingsarten der Drahtwüımer vertreten, wobei 12 Arten von ihnen Massenvermehrung eigen ist. Diese Schädlinge kommen in allen Zonen and allen Böden vor und machen die Hälfte aller Bodenschädlinge aus. Die stärkste Verbreitung weisen *Selatosomus latus* und *Agriotes sputator* auf, wobei ersterer 32% und der zweite 37% der Ackerböden beherrscht. *Agriotes gurgistanus* besiedelt 23% und *Agriotes ustulatus* 17,5% derselben.

Verbreitungsgebiete der einzelnen Arten werden von den Bodenbeschaffenheiten bestimmt und fallen mit den Grenzen der Bodentypen zusammen. Für die einzelnen Bodentypen in verschiedenen Zonen ist bestimmter Artenbestand der Drahtwürmer charakteristisch. Die Verbreitung der einzelnen Arten hängt von den mechanischen Bestandteilen sowie der Feuchtigkeit des Bodens ab.

Nach ihrer Ernährungsdynamik und Schädlichkeit werden die Drahtwürmer in zwei oekologische Gruppen eingeteilt. Zu der ersten Gruppe zählen die meisten *Selatosomus*-, *Athous*- und *Limonius*-Arten. Zu der zweiten Gruppe gehören die meisten *Agriotes*-Arten. Schädauftıeten der Drahtwürmer der zweiten Gruppe verlauft in der Regel alljährlich, und zwar fast ungeachtet der Fruhjahrswitteıungverhältnisse.

Massenauftreten der Drahtwürmer der ersten Gruppe ist nur in Jahren mit warmen kurzen Frühlingen zu beobachten, da die Frühlings-Futterungsperiode kurz und bei langem kaltem Frühjahr vor der Aussaat zu Ende ist.

Auf Gıund ihrer Nahrungsbeziehungen können die Schädlingsarten in 3 Hauptgruppen eingeteilt werden. 1. Die *Agriotes-Adrastus*-Gruppe. Vorwiegend phytophag und saprophag, räuberisch durch Zufall—bedingt durch Lebensverhältnisse. Polyphag und schädigen fast sämtliche Kulturen, bevorzugte Nahrungsmittel aber sind Würzeln sowie andere unterirdische Organe der Gıas- und Getreide-Arten. Noımale Entwicklung auch ohne tierische Nahrung. 2. *Selatosomus-Athous* Gruppe. Phytophag und räuberisch. Bevorzugtes Futter: Samen, Knollen und Früchte, kleine Insekten, vorwiegend wenig bewegliche, am haufigsten Puppen und Larven in Häutung. Normale Larvenentwicklung ohne tierische Nahrung unmöglich. 3. *Melanotus-Ortathous*-Gruppe. Vorwiegend räuberisch. Fügen auch grossen Schaden verschiedenem Saatgut sowie Knollen, Kornerfrüchten, Zwiebeln u.a.zu. Ziehen jedoch räuberische Lebensweise vor. Normale Larvenentwicklung ohne tierische Nahrung unmöglich.

Die Untersuchungen der Nahrungsbeziehungen der Drahtwürmer erfolgten in Laborverhaltnissen und fanden ihre Bestatigung in der Natur. Diese Ergebnisse rücken die Bedeutung der Larven in den Ackerbodenbiozönosen in ein neues Licht. Auf solche weise müssen diese Arten nicht nur als Pflanzenschädlinge, sonder auch als nutzliche Bodenorganismen betrachtet werden. Aus diesem Grunde sollten die Massnahmen gegen die Drahtwüımer dieser Gruppen nicht auf ihre vollige Vernichtung, sondern nur auf die Verringerung ihrer Zahl im Hinblick auf Saat guι- und Pflanzenschutz gerichtet sein. Diesen Forderungen entspricht die Methode der Samenbehandlung mit Insektiziden. Zur Saatgutbehandlung wurden Dieldrin, Gamma-Hexachloran, Heptachlor und Telodrin erprobt.

Die besten Ergebnisse wurden nach der Behandlung des Saatgutes mit Heptachlor-Emulsion erzielt, und zwar, wenn diese Massnahme wiederholt im Laufe einiger Jahre auf demselben Ackerabschnitt unternommen wurde. Die Zahl der Drahtwürmer verringert sich nach zwei Jahren um 8-10mal und es wurde möglich, überaus empfindliche Kulturen (Mais. Tomaten u.a.) zu ziehen.

RECENT STUDIES ON THE CONTROL OF SORGHUM INSECT PESTS IN INDIA

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Insect pests constitute one of the principal factors limiting production of sorghum, *Sorghum vulgare* Pers., over more than 40 million acres under cultivation annually. The major pests attacking this basic food crop include the shoot fly, *Atherigona indica* M., the stem borer, *Chilo zonellus* Swinh., the ear head midge, *Contarinia andropogonis* Felt, a Capsid ear head bug, *Calocoris angustatus* Leth., a Fulgorid hopper, *Peregrinus maidis* Fitch, an aphid, *Aphis sacchari* Zehnt., a mite *Oligonychus indicus* Hirst, and various species of ear head caterpillars, grasshoppers and soil insects. Of these probably the most important are shoot fly, stem borer, midge and the Capsid bug. The studies conducted to date have been concerned with the first two of these pests.

The shoot fly, *A. indica*, attacks the crop in the seedling stage, the adult fly depositing its eggs on the underside of the leaves, starting from soon after germination until about the seven leaf stage. The newly hatched larva migrates down the leaf sheath to the base of the plant where it cuts the central shoot, later completing its development on the decaying plant tissue produced in the "dead heart" above the cut. Affected plants produce tillers which may in turn be attacked. The crop loss results from a reduction in stand of healthy main shoots and the production of tillers which mature later and yield less grain and fodder than the original main shoots. This insect has been effectively controlled in experimental plots with 10% phorate granules applied to the seed furrow at the rate of 1·5-2·25 grams per meter of row. Foliage applications of commonly available insecticides have given partial though not effective control (1).

Varieties tolerant to this insect have been identified and the use of this tolerant germ plasm in the plant breeding program is being investigated.

The stem borer, *C. zonellus*, generally attacks sorghum after the sixth oı seventh leaf stage of growth. Eggs are deposited in masses on the underside of the leaves and the hatching larvae migrate to the whorl where their feeding may cause the central shoot to be killed, essentially removing the plant from production. When the central shoot is not destroyed, the tunnelling in the stems by the larvae reduce the yield of grain and fodder. Usually a single sorghum crop is attacked by two generations of the borer.

This pest has been effectively controlled with foliage applications of granular formulations of endrin (·2 Kg/ha. of active ingredient), carbaryl (1·5 Kg/ha.) and BHC (0·25 Kg. gamma/ha). Borer tolerant varieties have also been identified.

Research is being continued to develop appropriate control measures for these and other sorghum insect pests that can be used on improved varieties and hybrids.

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SOIL AND SEED TREATMENT WITH THIMET AND DI-SYSTON TO CONTROL COTTON INSECTS IN IRAQ

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Thrips tabaci Lind. is the most damaging pest to cotton seedlings in Iraq. *Aphis gossypii* Glov. is not as important because of low spring population. Leaf-chewing insects especially grasshoppers cause some damage to cotton in the spring. The spider mite *Tetranychus atlanticus* McGregor attacks cotton about the middle of May until the middle of July or after, damaging the leaves and weakening the plants. About the time the mite appears, two insects start their attack, these are the white fly *Bemisia tabaci* Genn. and the spiny bollworm *Earias insulana*

Boisd. Their population increases gradually, and that of the spiny bollworm continues until the end of the season.

Four years of experiments with Di-syston and thimet showed excellent control of the thrips, aphids, and later the control of early population of the spider mite, when these chemicals were applied to the seeds or soil at the recommended dosages at planting date.

While some effect of these chemicals was observed in reducing the amount of feeding by leaf-chewing insects and in reducing the numbers of the white fly, no effect was noticed in preventing the attack of the spiny bollworm. Reduction in the rate of seed germination was detected. Phytotoxicity was apparent but not serious.

PROBLEMS IN THE USE OF INSECTICIDES

INVESTIGATION ON EFFECT OF ACARICIDES AND RED SPIDER OVICIDES ON FLUCTUATIONS OF THE FRUIT RED SPIDER MITE (*PANONYCHUS ULMI* KOCH)

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In recent years an increase of the fruit tree red spider mite has been noticed in the orchards in Yugoslavia. Attacks were particularly intense on apple trees but they also occurred on peach, plum and pear. Investigations showed that there are eight generations of *P. ulmi* in a season under climatic conditions of NW Croatia.

Influence of the apple variety upon density of the population was examined and it was found *P. ulmi* prefers London Pippin. Examination of the efficacy of acaricides and ovicides was carried out in apple tree plantations of varieties: Lp, Jn, Bp and Cx. Density of the population was determined during the vegetative period by the Austin and Massee "imprint" method on an average sample of 50 leaves. Deposited winter eggs were determined on an average sample of 10 twigs, 1 inch long; the efficacy was calculated by the Abbott method.

During the 1963 winter, field trials were carried out against winter eggs with materials based on tetrachlordiphenylsulphide, formulation as w.p. and emulsion with 20% a.m. in 0·04% a.m. concentration. Comparison materials were based on DNOC—5% in yellow oil and 30% in paste form. Results showed a better efficacy of the tetrachlordiphenylsulphide, formulation w.p. The natural mortality was 57·8%.

A considerable number of acaricides were tested against *P. ulmi* as follows: Tetradifon, Phenkafos, Kelthane as selective acaricides. Tiometon, Dimetoat, Cidial as materials with endotherapeutic action. Special attention was paid to the efficacy of tetrachlordiphenylsulphide and indopol-polybuten 75% (Poly-Kil). Spraying was carried out after blossom (May 5th) and repeated on July 9th, when the population was very high again. Imprint recording was carried out between May 3rd and Sept. 14th.

The highest efficacy value was shown by Cidial/Phosphor-ester with 50% a.m. Similar results were obtained by the Dimetoat with 20% a.m. Tiometon 20% a.m. gave a very good protection but it had better results in combination with Tetradifon. The summer ovicide based on Tetradifon 20% a.m. also gave a good protection.

Especial attention is deserved by Tetrachlordiphenylsulphide w.p. with 20% a.m., concentration 0·04% a.m., efficacy value 96·8% with only two winter eggs deposited. Still better results were obtained by Indopol-polybuten 75% a.m., efficacy value 97·8%, number of winter eggs 1·4. Both these preparations were applied whilst the trees were in leaf, but caused no phytotoxicity to the apple trees.

Phenkafos 20% a.m. gave poorer results (91·12%) with the maximal number of winter eggs (516·6). Kelthane 25% had a poorer value (94·4%), number of winter eggs 13·8.

PESTICIDE RESIDUES AND PROBLEMS RESULTING FROM DRIFT FROM AERIAL APPLICATIONS OF DUSTS AND SPRAYS

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Aircraft application of pesticide dusts and sprays in the United States began about 1921. Since then the use of aircraft for applying pesticides has increased many times. From the beginning the drift of pesticides from application area to adjacent crops has been a problem, which has become more serious with the increased use of aircraft for pesticide application.

The amount of pesticide involved in the drift may not be a hazard to humans or livestock, but the small amount of residue on feed can contaminate the fatty tissues of meat animals or the milk of dairy animals. The secondary contamination is the point of concern of this study.

Food and Drug Administrations zero tolerances in many animal products together with the withdrawal of certain pesticide uses by various states, has prompted the drift studies in Arizona. Data obtained thus far, represent results from three large scale experiments.

Test No. 1: Toxaphene dust and spray was applied to a field of alfalfa by aircraft and allowed to drift on to another alfalfa field.

A drift line was established in each field with reference to the direction the wind carried the pesticide. Stations were established at 82, 165, 330, 660 and 2640 feet, at which replicate samples of alfalfa were taken and analysed for pesticide residue.

Test No. 2: Three pesticides, DDT, Toxaphene, and Tedion were applied by aircraft as dust and spray to cotton and drifted onto alfalfa. Sampling and residue analysis were the same as in Test Number 1.

Test No. 3: BHC and DDT, as dust and spray, were applied by aircraft to cotton and drifted on to alfalfa. Sampling procedures were similar to those outlined for Test Number 1. In addition alfalfa samples were obtained two miles downwind.

Results: The initial pesticide deposit on the target crop is greater for spray than for dust and measureable amounts of dust drift farther than sprays. The ratio of dust to spray increases with increasing distance. For example, at 82 feet downwind the residue of dust was 27 ppm and for spray 7 ppm or a ratio of 4:1, at 1320 feet the dust residue was 8 ppm and spray 1·4 ppm or a ratio of 6:1.

To have 2·5 ppm DDT in the butterfat of milk, would require alfalfa to have a DDT residue of 0·5 ppm or less. To obtain this, data indicate that alfalfa would have to be 2,100 feet downwind of a spray application and 6,200 feet of a dust application of 2·5 lbs. DDT per acre. Since only 1·25 ppm or less DDT is allowed in the butterfat, alfalfa would have to be 3,000 feet downwind of a spray and 8,000 feet downwind of a dust application.

Dissipation curves indicate that fresh alfalfa which has an initial contamination of 20 ppm DDT, will have only 2-3 ppm 14 days later. Data also indicate the pesticide residue of baled hay is increased during the curing and baling process. This is due to the loss of water in the plant and lack of absolute amounts of pesticide residue.

ON THE BARK TREATMENT WITH METHYLDEMETON (METASYSTOX)

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Bark treatment by painting with methyldemeton (P=O Metasystox, 25%) is recognised as a useful method for controlling aphids and red spider mites in Japan. The outline of my study concerning the painting has already been reported (Japanese Journ. App. Ent. Zool., vol. 8, no. 1, 1964), however there is a troublesome problem with this method concerning phytotoxicity or bark injury to citrus trees when undiluted emulsion is used. I consider that the main factors contributing to bark injury may be as follows:

(1) Thick painting or heavy dosage per unit area of bark, not the total dosage applied to a tree.

(2) High temperature at the painting time as well as for several hours after treatment.

From the combination of two main factors, we can estimate the safe range for bark injury. In the case of light painting (0·6 cc/100 cm^2), the safe upper temperature limit is considered normally to be 27°-28°C. so far as the temperature in painting time is concerned. However, as a practical problem, the diurnal change of temperature must be considered, so various further experiments have been carried out. From these experiments I consider that high temperatures continued for a long time after painting are most dangerous, but that high temperatures after cool conditions are not so dangerous as long as the post-painting low temperature continues for some 10 hours or more. This problem can be related to painting time. In the case of morning painting the temperature is not so high at the painting time, but it will be higher in a few hours in general. Therefore, the morning treatment is not always safe. However, it may be said that evening painting is far safer as low temperatures normally follow application.

As a conclusion I recommend "light" painting in the evening to prevent bark injury. Of course, use of diluted emulsion is safer for painting, but I think that the undiluted chemical may also be used under the conditions mentioned above except in mid-summer.

RATIONAL PEST CONTROL, CHEMICAL AND BIOLOGICAL: (1) USE OF NATURAL ENEMIES

INFLUENCE OF PREDATION OF *COCCINELLA SEPTEMPUNCTATA* ON *APHIS FABAE*

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The advantage of coccinellids as natural enemies of aphids is that larvae as well as adults are aphidophagous, and that the coccinellids search for their prey at random. For these reasons they can kill also single aphids right at the beginning of the infestation of fields. And just this critical period is the only possible time when, under certain conditions, the natural enemies can prevent the aphids from the detrimental overpopulation. (As overpopulation develops the natural enemies are no longer of much help.)

Effectiveness of coccinellids in the control of aphids in that critical phase depends partly on their quantity, partly on weather conditions. To clarify this dependence we made two successive field-cage experiments in the years 1963 and 1964.

In 1963 in the critical phase of middle June the weather was much colder than in the analogous period of early June in 1964. During the first 10 days of the experiment in 1963 the average temperature was 16·7° and the average of daily maxima was 21·3°, in the year 1964 the average temperature was 19·5° and the average of daily maxima 26·1°C.

The different temperature had a striking influence on the results. In the colder conditions of the year 1963 at least 1 coccinellid to 30-60 aphids was necessary to prevent them from overpopulating. When 1 beetle came to 100 or more aphids, the coccinellids could not substantially cut back the increase of the population density of the aphids.

On the contrary, in hot conditions of the year 1964 the coccinellids were able to liquidate the infestation of sugar beet by aphids, although at the introduction of the beetles the ratio was of 1 coccinellid to 200 aphids.

We presume that the different issues of the years 1963 and 1964 resulted from the combination of two effects of the higher temperature on the relation between the aphids and predators: favourable for the feeding capacity of the coccinellids, and unfavourable for the reproductive capacity of *Aphis fabae*.

ACCLIMATATION DE *CRYPTOLAEMUS MONTROUZIERI* MULS. EN SICILE ET LUTTE BIOLOGIQUE CONTRE *PSEUDOCOCCUS CITRI* R.

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Pseudococcus citri R. est fréquent dans les plantations d'agrumes de la Sicile et il est très difficile à combattre efficacement avec les insecticides chimiques.

D'autre part, des expériences de plusieurs dizaines d'années faites en Califoınie (Riverside) et même actuellement en Espagne, ont montré que cette cochenille peut être combattue avec de bons résultats au moyen du "Coccinellidae *Cryptolaemus montrouzieri* Muls."

Ce prédateur, decouvert en Australie par Koebele en 1890, fut introduit en Californie en 1892, et en Europe en 1908 par Silvestri qui tenta de l'introduire en Italie. D'autres de tentatives d'acclimatation furent faites en France en 1918 (Poiciers, 1923) en Egypte en 1922 (Hall, 1927), en Palestine en 1925 (Bodenheimer, 1951) et en Espagne en 1926 (Gomez Clemente, 1932). En Sicile, après celui que Silvestri effectua en 1908, d'autres lancements de *Cryptolaemus* furent faits en 1935 et en 1936 par l'Observatoire Phytopathologique dans les environs de la ville (Montemartini 1936) et de la Station d'Agıumicultuıe d'Aciréal dans les provinces de Catane, Enna et Syracuse (Costantino 1935).

Toutes les tentatives faites jusqu'à aujourd'hui pour élever et répandre le prédateur ont eu peu de succès sauf en Espagne, où existent encore des élevages dans des insectaires appropriés, et en Califoınie.

Les essais d'acclimatation n'ont donné en Francc un résultat positif que dans la région niçoise (Marchal, 1922); ils ont échoué en Palestine (Bodenheimer, 1951), en Algerie et en Egypte (cfr. Grandi, 1951). En Italie, malgré des lancements repétés de *Cryptolaemus* effectués, comme nous l'avons dit, dans des zones variées, toujours d'après Silvestri (1939), l'acclimatation ne se fit que sur la Riviera Ligure.

Cependant, récemment, à la suite des observations faites en plein champ en 1935 dans les plantations d'agıume de Palerme (Monastero et Zaami, 1959) et au course des années 1959-60-61 et 63 (Liotta et Mineo, 1963) sur le territoire de Bagheria, on peut affirmer que ce prédateur s'est acclimaté aussi en Sicile.

Toutcfois, il faut ıemarquer qu'il a été toujours retrouvé en nombre très limité, si bien qu'il ne peut pas devélopper une action économiquement appréciable contre le *Pseudococcus citri* R. A cause de ces considérations, en collaboration avec mon collégue Doct. Mineo, utilisant la technique suivie en Californie et en Espagne, nous avons commencé en 1963, dans les insectaires de l'Institut d'Entomologie Agraire, un élevage en masse du prédateur dans le but de lancer un grand nombre d'exemplaires au moment opportun, dans les plantations infestées par le *Pseudococcus citri* R. (*Lutte biologique artificielle*, selon le terme employé par Monastero, 1963).

Les adultes de *Cryptolaemus*, dans les champs, au cours de l'été, se sont multipliés normalement et les larves, avec les adultes, ont désinfesté totalement les arbustes, en se déplaçant toujours davantage à recherche d'un autre *Pseudococcus*. Sur un plant d'agrumes, j'ai compté plus de 2000 larves de *Cryptolaemus*.

Comme il sera publié plus longuement dans un prochain travail, le *Cryptolaemus* effectue dans les champs au moins quatre générations annuelles et il hiverne, en Sicile, au stade de, larve et d'adulte.

Des observations faites, on conclut que le *Cryptolaemus montrouzieri* s'cst acclimaté en Sicile qu'il passe l'hiver au stadc de larvc et d'adulte et que sa réduction numérique en hiver, est due principalemcnt à l'absencc d'hôtc.

TELENOMUS TEREBRANS RATZ., PARASITE DES OEUFS DU BOMBYX A LIVREE (*MALACOSOMA NEUSTRIA* L.)

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Au cours des dernières années, dans certaines localités et leurs environs (Svetozarevo et Leskovac), en Yougoslavie, le Bombyx à livrée fait régulièrement son apparition sur les pommiers. Dans ces recherches une attention particulière a été portée sur l'espèce *T. terebrans*, d'une part à cause de son activité dans la réduction de la population de la livrée, et d'autre part, au point de vue scientifique, à cause de certains moments intéressants du développement de ce parasite.

Au cours de trois années, d'un total de 79,192 oeufs, 2·9% avaient été parasités. Cependant, il serait erroné de considérer que cela représente l'efficacité de *T. terebrans* dans la pleine réduction de la population de la livrée. En 1963-64, l'analyse détaillée et la dissection des oeufs et des chorions, après la fin de l'apparition des parasites, ont montré qu'un grand nombre de parasites se développent normalement dans les oeufs de la livrée jusqu'au stade d'adulte, mais qu'ensuite ils périssent sans abandonner le chorion ou juste en l'abandonnant. Ce phénomène a été constaté chez *T. laeviusculus*, dans les environs de Moscou (1), et cet auteur considère qu'il a lieu quand l'air est trop sec au moment des éclosions des adultes du parasite. Nous croyons pourtant que cette manifestation pourrait s'expliquer aussi par la structure mécanique du chorion des oeufs du Bombyx à livrée, sensiblement épaissi à sa partie supérieure, ce qui empêche l'adulte formé d'abandonner le chorion. Cette hypothèse est égalment confirmée par le fait que les adultes qui délaissent les chorions se trouvant sur la périphérie des bagues, le font toujours sur la face latérale des chorions où les parois sont beaucoup plus minces et permettent aux parasites d'y percer l'ouverture de sortie avec moins d'efforts.

Les données obtenus indiquent que de 30,443 oeufs dans 120 bagues d'oeufs, soit 21·17% ont été parasités au cours de 1963-64. Il faut particulièrement faire ressortir que de 6,447 oeufs parasités, il est sorti 3,169 adultes du parasite et que 3,278 adultes ont été trouvés morts dans les chorions des oeufs. Dans chaque oeufs il ne c'est développé qu'un seul parasite. Le pourcentage d'oeufs parasités dans une bague a varié de 0-88,2%

Par conséquent *T. terebrans* représente donc un facteur actif dans le cadre du complexe des insectes entomophages du Bombyx à livrée.

Début et rythme de l'apparition des adultes de T. terebrans. La donnée la plus interessante est sans nul doute la période très concentrée d'apparition des parasites. C'est ainsi qu'en 6 jours (du 3 au 8 juin 1963) il est sorti 2,056 adultes du parasite, soit 97%, tandis que dans la période ultérieure d'apparition en 12 jours (du 8 au 20 juin) il est sorti en tout 72 adultes, soit 3%. Cette période concentrée d'apparition des adultes du parasite pourrait jouer un rôle important en cas d'utilisation pratique de *T. terebrans*.

Rapport des sexes chez T. terebrans. Pour les espèces de parasites des oeufs du Bombyx à livrée, constatées dans l'Union soviétique, signale que leurs mâles n'ont pas été trouvés à Moscou, tandis que dans d'autres localités ils ont été rencontrés en petit nombre. C'est ainsi que pour l'espèce *T. laeviusculus* il a été constaté le rapport M: F = 1:100.

Au commencement de ces recherches nous avons également constaté un très petit nombre d'exemplaires mâles dans la population de *T. terebrans*, si bien que cette question a éveillé chez nous aussi un intérêt particulier. L'index sexuel montre également la grande participation des femelles dans la population = 0,95. Et malgré cela, d'année en année, la population de *T. terebrans* se multiplie normalement dans la nature. Ce phénomène pourrait s'expliquer de deux manières: par la possibilité de la fécondation d'un plus grand nombre de femelles par un même mâle ou bien par la multiplication parthénogénétique.

Dans ces expériences un autre problème s'est encore posé: Est-ce que peut-être les adultes du parasite, formés dans les chorions et qui ensuite périssent sans essayer d'en sortir ou bien au moment-même où ils les abandonnent n'appartiennent pas à un seul sexe. C'est dans ce but que, dans la chambre acclimatisée, une expérience a été faite avec 50 bagues d'oeufs recueillies dans la nature quelques jours auparavant. Il a été constaté ce qui suit:

1. Dans les conditions favorables de la chambre acclimatisée il s'produit une interruption de la diapause chez les larves adultes hibernantes de *T. terebrans*, se sont chrysalidées et ont

donné des insectes adultes, ce qui signifie qu'on peut obtenir, au cours de la longue période d'hibernation, du matériel pour le travail expérimental.

2. Le rapport des sexes dans ce matériel a confirmé les constatations antérieures, d'après lesquelles les femelles ont une participation beaucoup plus grande dans la population de *T. terebrans,* parmi ces exemplaires qui ont abandonné les chorions. Mais, le rapport des sexes parmi les adultes ayant péri dans les chorions n'a pas confirmé hypothèse que la mortalité ne frappe qu'un seul sexe, car par la dissection nous avons pu constaté un bien plus grand nombre de femelles que de mâles.

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LES RESULTATS DE LA LUTTE BIOLOGIQUE ARTIFICIELLE CONTRE *DACUS OLEAE* AU MOYEN DE *L'OPIUS CONCOLOR* SZEPL. ET DE *L'OPIUS CONCOLOR SICULUS* MON.

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La "lutte biologique artificielle" consiste dans l'élevage "en masse" dans des insectaires spéciaux de parasites spécifiques et monophages d'une espèce phytophage, pour le lancement dans un moment opportun, d'un grand nombre de ces parasites, même dans les milieux où l'espèce parasitaire existe déjà. (1). Cette lutte se distingue de la lutte biologique classique que nous pouvons définir "naturelle" (2).

Il nous a été possible d'élever en continuation dans nos insectaires spéciaux dès 1959 les *Opius concolor siculus* Mon. et *Opius concolor* Szépl. sur les larves de *Ceratitis capitata,* avec une moyenne de 18 générations par an (3, 4, 5). Ces élevages nous ont permis de faire les premières introductions des *Opius* en 1961 et 1962 (3, 4).

Encouragés par les résultats précédents, en 1963 nous avons fait une expérimentation plus importante dans l'île de Salina (au nord de la Sicile). Nous avons choisi une plantation de 10,000 oliviers de l'île (total ca. 25,000 plantes).

Pour le contrôle, nous avons choisi les olivettes de deux zones diverses de l'île de Salina et celles de l'île de Lipari qui se trouve à quelques km de Salina.

Selon nos examens, la première infestation dans la plantation de Rinella (Salina) a été trouvée pendant la seconde décade de Juillet avec 0·66% de larves jeunes, tandis que dans les autres plantations d'oliviers de la meme ile les olives étaient encore complétement immunes ou présentaient un pourcentage minimum de piqures stériles.

L'échantillonage successif après 10 jours (30 Juillet) présentait quelques rares pupes et des larves de premier et deuxième stade, dont quelques-unes sont mortes pour des raisons inconnues.

Le 10 Août, outre les larves en premier et deuxième stade il y avait un pourcent de larves en troisième stade et 2,24% de pupes vivantes et pupaires vides. Le 20 Août l'infestation totale était de ca. 7,3%.

Dans les autres olivettes de la même île, l'infestation était en retard en comparaison de celle de Rinella n'arrivant qu'à 2,50% au total. A la meme date à Lipari l'infestation était de 0·7%.

Dans ces condictions nous avons jugé opportun de fixer le premier lancement le même jour, 20 Août, en lâchant 18,000 adultes de notre insectaire, soit 1.8 *Opius* pour chaque olivier ou 15.000 olives selon la charge moyenne par plante avec libération au centre de la plantation en question.

Pendant la troisième décade d'Août et pendant tout le mois de Septembre, l'infestation s'est maintenue égale ou légèrement inferieure à celle qui a été constatée le 20 Août, soit 7% environ.

A la fin de Septembre, 40 jours après le lancement, l'échantillon prélevé dans la zone de Rinella avait une infestation dacique de 17,50% tandis que dans les autres échantillons de la

même date des différentes zones de contrôle de Salina et de Lipari l'infestation totale était de 50%.

Pour ces raisons, le 18 Octobre nous avons décidé de lâcher 18,000 *Opius* adultes dans la même zone de Rinella. Malgré ça vers la fin d'Octobre les olives de la zone de Rinella montraient une infestation de 76%. Dans les zones de contrôle, y compris les olivettes de l'île de Lipari, presque le tiers des drupes étaient tombées à cause de l'infestation dacique, tandis que sur les arbres on pouvait constater une infestation de plus de 100% parce que les olives avaient deux ou plusieurs larves ou trous de sortie. Fin Novembre, dans la zone de Rinella également l'infestation était arrivée à 100%.

Il faut pourtant souligner que dans cette zone, pendant les mois de Septembre, Octobre, Novembre il n'y avait pas de perte d'olives et la maturation était parfaite; tandis que dans les zones de contrôle la récolte s'est terminée à la fin d'Octobre ou pendant les premiers jours de Novembre. Dans la zone de Rinella, les olives sont restées sur les arbres pendant tout le mois de Novembre et la récolte a continué jusqu'au 15 Décembre.

Nous pensons donc pouvoir constater que les *Opius* lâchés par nous même, malgré le nombre très limité en comparaison des olives présentes (rapport de 1:15,000 environ) ont notablement retardé l'infestation dacique dans la zone expérimentale.

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FURTHER PROOF OF PROTECTION AFFORDED BY *AZTECA* ANTS TO THE IMBAUBA (*CECROPIA*) TREES OF BRAZIL AGAINST INSECT PARASITES

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Azteca ants are vegetarian monoecous occupants of the hollow stems and trunks of *Cecropia* in South-East Brazil. They feed on the Müllerian fat-bodies developing at the petiole-bases and the tissue growing over the bore-holes. Early observers considered this symbiosis, but Ihering, who contested this view and said *Azteca* was a mere parasite, was followed by Wheeler. Eidmann later by experiments shewed *Azteca* defends its home against *Atta sexdens* leaf-cutter ants and claimed the relationship was symbiosis. He did not experiment with *Cecropia's* most serious parasite, the monophagous beetle *Coelomera lanio*, nor the several species of Lepidoptera found regularly on *Cecropia*, and his observations lasted two months.

The author's observations of tree and ant and parasites lasted from February 1958 to February 1959. In an experiment, fifty small *C. lanio* larvae were attached to a sapling less than 1 metre high but already colonised by *Azteca*. Ten days later there were thirty dead but not a living larva remained. Control *lanio* larvae pupated about 1 month after hatching from egg and mature beetles emerged about 2 weeks later. Thus comparatively few *Azteca* successfully defended their young and vulnerable host from an enemy army which would have destroyed it.

Normally *C. lanio* oviposits on *Cecropia* about 2 metres high. The masses sometimes inflict great damage before leaving such trees to pupate, but damaged trees at this stage were observed to recover eventually; the ant colonies were inactive during the infestation and for weeks later; starvation due to *C. lanio's* depredations may be responsible. The *Azteca* colony in a healthy tree is active normally over a hundred years.

Larvae of the Nymphalid butterfly *Gynecia dirce* L., polyphagous on trees, were repeatedly seen on *Cecropia* but only in the sapling stage before ant activity became intense. Young

larvae observed on some saplings with lively *Azteca* colonies disappeared before reaching one-third growth; at this stage the *dirce* larva forms a tent by half-cutting a leaf-rib. More than six freshly hatched *dirce* larvae were never found, nor more than three full-grown, on a single Imbauba.

Larvae of the moth *Dyops ocellata* F. feed in masses but were less often seen than either *dirce* or *lanio*. They seem to be monophagous on Imbauba, and like *lanio* might inflict fatal damage on saplings. Probably *Azteca* would destroy *Dyops* as it did *lanio*. It may also thin out the less dangerous *dirce* larvae.

Azteca is not tolerant but hostile to those parasites of the tree which are numerous and destructive; however, it is not always successful against its enemy. Nevertheless, a symbiosis, advantageous to tree and ant, has again been proved to exist, confirming the interpretation of Müller and Eidmann.

(A longer account of these observations will appear elsewhere.)

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(2) SELECTIVENESS IN PEST CONTROL BY CHEMICALS

STUDIES ON BEE POISONING IN GREAT BRITAIN

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The losses of honey bees from pest control operations in Great Britain is not a very serious problem. In recent years, the greatest number of reported losses was in 1959, when over 700 colonies were seriously affected. This was exceptional, as usually there are less than 300 from the total estimated number of 300,000 bee colonies in England and Wales. In spite of this, the loss to individual bee keepers may be serious; one in Norfolk losing an estimated one ton of honey as a result of parathion poisoning.

The insecticides currently responsible for deaths of bees in Great Britain are organophosphorus compounds, dieldrin, lindane and the carbamates. This is in contrast to the findings of a survey in 1948 (Glynne-Jones) when the main compounds responsible were arsenicals, DDT and DNOC.

Another interesting difference between the present survey and that of 1948 is the type of pest control operation responsible for the deaths of bees. In 1948 it was reported that the majority of bee casualties were the result of pest control activities in fruit growing areas; now deaths are due to the spraying of arable crops in East Anglia. All the cases of poisoning in East Anglia were found to be due to organophosphorus materials. Of 20 cases involving 208 colonies poisoned by organophosphates in 1963, the evidence indicates that 11 were killed by dimethoate, four by demeton methyl, two by phosphamidon and in the remaining three cases, there was no evidence available for identification. Of these 20 cases of organophosphate poisoning, 14 were killed by the spraying of field beans, 10 of these being the result of aerial spraying. There is a tendency to spray this crop when an infestation is established which, if the crop is in flower, is harmful to bees to whom bean flowers are particularly attractive.

The chlorinated hydrocarbon insecticides are potentially extremely hazardous to bees but few cases of poisoning from DDT and lindane are encountered and it is dieldrin which is responsible for most bee deaths. There were 8 cases in 1963. In our experience the spraying of mustard when in flower is the only agricultural application of dieldrin which is responsible for damage to bees. In 1960 100 colonies were seriously affected by this use of dieldrin.

Another major hazard to bees from dieldrin is caused by wasp baits, consisting of candy and dieldrin, which are placed around bakeries and other places where wasps are a nuisance. The candy is initially hard and is supposed to be selective in its action because wasps with strong biting mouth parts can consume it whereas bees cannot. In practice the candy, being deliquescent, soon becomes soft enough to be available to bees. Dieldrin from these wasp baits has, on one occasion, been found in honey; the amount was small, only 0·04 ppm.

Carbamates are responsible for the deaths of some bees and the evidence seems to indicate that the danger arises when the carbamates are sprayed on to apple trees for fruit thinning purposes as it may be applied when there are still some flowers on the trees.

Weedkillers and fungicides are sometimes suspected of killing bees and a few cases of poisoning by these pesticides have undoubtedly occurred. One case of poisoning by a weedkiller concerned sodium monochloroacetate which was believed to be safe to bees. Investigations showed this to be true as far as the contact toxicity of the weedkiller was concerned but oral toxicity was found to be high. Thus insects drinking from collections of spray droplets in leaf axils would receive a toxic dose. This was only an isolated incident, but it illustrates the advisability of investigating all the possible routes of poisoning before regarding a pesticide as "safe" for beneficial insects.

From this summary of our investigations into the causes of bee poisoning, it is clear that, out of the large number of insecticides which are potentially hazardous to bees, in practice relatively few kill them. Those insecticides which do not kill bees in the field must be exercising some selective effect by virtue of the manner in which they are used. A simple example of this selectivity is lindane, which is highly toxic to bees. In the season 1962/3 some $2\frac{1}{2}$ million acres were estimated to have been treated with lindane. None of this killed bees because over $2\frac{1}{4}$ million acres was in the form of seed dressings; a method of application which is selective in protecting insects on the aerial part of treated plants.

Our findings also illustrate another, perhaps more important, example of the effect of the method of application of the insecticide. Demeton methyl and dimethoate are both used extensively on field beans and, although no accurate figures are available, it is generally believed that the use of demeton methyl exceeds that of dimethoate. However our investigations show a greater hazard to bees from dimethoate, eleven cases to four of demeton methyl last year. Thus, when used in the field, demeton methyl may be less toxic to bees. All the four cases of demeton methyl poisoning were the result of aerial spraying which might serve to suggest that insecticides applied from the air are more hazardous to bees than when applied to crops by other means.

STUDIES TOWARDS AN INTEGRATED CONTROL PROGRAMME OF CITRUS PESTS IN ISRAEL

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An extensive, country-wide survey of citrus groves has yielded 55 species of Hymenoptera parasitic in citrus scale-insects and aphids. Of these 42 are primary, 13 are secondary parasites; 30 are new to the fauna of Israel. Considerable changes took place in the parasite fauna during the last 20 years or so. Several species, including *Aphytis coheni* DeBach and *A. lepidosaphes* Compere, have spread naturally into Israel, or otherwise were unwittingly introduced. *Metaphycus flavus* (Howard), having been very rare in the past (4), has recently risen to a major position (9). *Encyrtus lecaniorum* (Mayr) and *Aphytis chrysomphali* (Mercet), very abundant previously, were later largely displaced by other species.

The scale-insect pests, *Chrysomphalus aonidum* (L.), *Coccus hesperidum* L. and *Pseudococcus citriculus* Green, are efficiently controlled by parasites in Israel's citrus groves. The insecticidal check method (5, 6) was employed to evaluate the role of natural enemies in the regulation of

Aonidiella aurantii (Mask.) populations on citrus. Comparison between untreated and DDT-sprayed plots revealed that natural enemies—*Aphytis* spp. and *Chilocorus bipustulatus* (L.) – play a decisive role in preventing the build-up of the scale's populations at the beginning of summer. Suppression of these enemies at that period may result in severe outbreaks of the pest.

A significant rise of *Ceroplastes floridensis* Comst. in the same DDT-sprayed plots indicated the possible importance of natural enemies in the control of this serious pest.

Pesticides suggested for use against citrus pests were regularly tested in the laboratory for possible effects on parasitic Hymenoptera. *Aphytis holoxanthus* DeBach, an introduced, efficient parasite of *Chrysomphalus aonidum*, was used in these tests. These were conducted by two methods: (1) Recording adult parasite mortality as caused by forced contact with pesticide residues on treated citrus leaves in modified Munger cells (2, 3); (2) Comparing fecundity of female parasites confined in plastic capsules, glued on to pesticide-treated citrus fruits, artificially infested with *C. aonidum*.

The following pesticides proved harmless to the parasite: Zineb, 0·1% of WP 65*; Tedion, 0·2% of EC 8*; Kelthane, 0·2% of WP 18·5; Chlorobenzilate, 0·1% of EC 25; "Phenkaptone" (10), 0·1% of EC 20; "Zinc Metiram" (7), 0·2% of WP 80; "Kepone" (8), 0·1% of WP 50; and medium mineral oil. The following had a detrimental effect: Sulfur (dust, and 1% of WP 90); "Rogor" (10), 0·25% of EC 40; "Delnav" (10), 0·1% of EC 50; Ethion, 0·2% of WP 25 and 0·1% of EC 50; and the Malathion/protein-hydrolysate fruit-fly bait formulation (1). All mineral dusts tested, whether the pesticidal ingredient (Sulfur, Zineb, etc.) or the inert carrier, were found to be highly detrimental to the parasite.

A large-scale field study, covering 25 citrus groves, has shown that the aerial application of poisoned baits against the Mediterranean fruit fly, *Ceratitis capitata* (Wied.), had no greater detrimental effects on the natural enemies of citrus scale-insects than the alternative, less feasible, ground application of the same baits (1).

* WP=Wettable powder; EC=Emulsifiable concentrate, the figure representing percentage of active ingredient.

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PARASITE-HOST RELATIONSHIPS IN SPRAYED AND UNSPRAYED FIELD PLOTS

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Population studies of the leaf miner, *Leucoptera meyricei* Ghesquière and its parasites were made over a period of 40 consecutive weeks during 1960-61 in four experimental blocks of coffee, two of which received several applications of parathion sprays and the other two none. Each week eight different trees within each block, making a total of 32 trees, were covered with a tent, pyrethrum spray atomised within, and the adult *L. meyricei* and parasites recovered from the polyethylene sheeting used as a floor to the tent. Fortnightly, counts of leaves, mined and unmined, and collections of leaves with leaf miner larvae and parasites within them were made

to obtain additional measurements of the populations and parasite-host relationships. These intensive studies were supplemented with two special spray tests, in which different dosages of insecticides were used, and with collections of leaves made periodically over a rather extensive area in Kenya, from which adult leaf miners and parasites were reared to gain information on the parasite-host relationships over a wide range of ecological conditions.

The parathion sprays, one pound of 20 per cent wettable powder in either 65 or 80 gallons of water per acre, as used in the two experimental blocks, appeared to kill all adult leaf miners and parasites present. Possibly between 50 and 75 per cent of the leaf miner larvae and appreciably fewer of the immature stages of the parasites within the mines were killed. The sprays apparently had even less effect on the leaf miner pre-pupae and pupae and the parasites within the cocoons, which are usually formed in the litter and in crevices in the soil.

Leaf miner populations within the sprayed blocks were somewhat lower than those in the unsprayed blocks but the fluctuations were remarkably similar. This was also true in general for the parasites as well.

Assessment of the effects of the sprays on the efficiency of the parasites was made on the basis of the ratios of adult parasites to moths obtained from tented trees and from infested leaf samples held for adult emergence, as well as in terms of percentages of larvae parasitised in the samples dissected. It was found that the sprays killed a greater proportion of the leaf miner larvae than of parasites within the mines and thus increased the ratios of living parasites to leaf miners immediately following the spray applications. During the period from October to January, when the sprays in the Rukera plots were synchronised with the peak populations of the moth, parasitisation was significantly higher in the sprayed plots than in the unsprayed plots. Furthermore, in the special spray tests, where different dosages of parathion and diazinon were used, parasitisation within the survival populations was higher in the plots that received the higher dosages. These findings suggest that with proper timing of spray applications the efficiency of leaf miner parasites may be improved.

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SEVERE OUTBREAKS OF CATERPILLARS ON OIL PALM ESTATES IN MALAYA INDUCED BY THE USE OF RESIDUAL CONTACT INSECTICIDES

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Many potentially serious pests of agriculture are held in check by insect natural enemies. The latter appear to be particularly important in the wet tropics, especially in the stable conditions of perennial plantation crops, where the physical environment regularly favours pest increase. The use of contact insecticides in these circumstances can, by killing these insect enemies, lead to outbreaks of a severity unprecedented in the particular situation. This is illustrated by the experience of three Malayan oil palm estates. On all of them, following the use of contact insecticides, severe outbreaks of caterpillars, mainly in the families Psychidae (bagworms) and Cochlidiidae (nettle or slug caterpillars), occurred over several thousand acres, leading to severe defoliation and hence crop loss. In some cases such chemicals were applied against cockchafer beetles, a relatively minor problem, or against limited outbreaks of bagworms. Early attempts to control the outbreaks by further spraying only worsened the situation since initially spray methods were poor and there was little kill of caterpillar pests to compensate for the elimination of insect enemies. Subsequently effective techniques were developed and control was achieved, but outbreaks continued to develop around the sprayed areas, probably due to the drift of chemicals in doses lethal to natural enemies, and eventually in the sprayed area itself. On one estate in Central Johore the whole 6,000 acres was sprayed, many areas receiving several applications in a two-year period. Eventually outbreaks which would, on recent standards, have involved the spraying of some 800 acres against bagworms, were left untreated. Parasitisation rapidly increased and the infestation declined. No

further spraying has been required on the estate. On another estate in Perak, applications of contacts commenced in 1956 and in every subsequent year, except 1958, between one and two-and-a-half thousand acres have been treated with endrin. Spray programmes are still in progress there. On the third estate, outbreaks which followed dieldrin sprays have now been successfully treated with lead arsenate.

In all cases, although certain species may have been dominant, several other species in these families have been present in the outbreaks. In the case of bagworms, the species initially present in limited numbers was not the one which built up heavily following the commencement of spray programmes. The estates are in quite different localities and these problems commenced at different times.

A modification of DeBach's insecticidal check technique has illustrated the value of natural enemies in the control of the bagworm *Metisa plana* Wlk. Distinct increases in this pest were recorded in and around a two-acre plot given dieldrin sprays at low dosage with partial coverage.

Lead arsenate is an effective integrated control. It is known to have at most only slight toxicity to natural enemy species. It was found to be effective at 3-4½ lbs. per acre against caterpillar pests. It has been used experimentally and in full-scale control without resurgences occurring.

Severe pest outbreaks following the use of contact insecticides against relatively minor problems have also been noted in tea and cocoa and in other oil-palm estates in Malaysia.

There is an apparent need to increase knowledge of the factors influencing pest numbers in tropical conditions and to develop integrated control techniques for such pests as do increase.

(3) AGRICULTURE AND THE BIOCOENOSE

PARTICULARITES DE LA FORMATION DES AGROBIOCOENOSES DE BLE LORS DE LA MISE EN CULTURE DES STEPPES NATURELLES AU KAZAKSTAN

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Selon l'auteur, la biocoenose est la seule forme d'existence possible des organismes autotrophes et hétérotrophes. En dehors de la biocoenose, l'existence de l'espèce est possible seulement en expérimentation.

Les biocoenoses cultivées ou agrobiocoenoses possèdent la propriété la plus importante de toute coenose: la constance des espèces constantes et dominantes dans le temps et l'espace (Bei-Bienko, 1961) et la capacité d'autorégulation. Les agrobiocoenoses de blé se caractérisent, déjà dans la première année après le défrichement, par des complexes de faune particuliers aux champs de blé d'une zone géographique donnée. Leur formation a lieu dans les conditions de sélection sévère et de labilité écologique. Dans les premières années de formation on constate des écarts dans les proportions quantitatives entre divers groupes de faune et un niveau général élevé de population. Une très grande supériorité numérique de dominantes en oligophages nuisibles s'accompagne d'une très faible quantité de population d'ennemis naturels, arthropodes parasites et rapaces. Ce phénomène rend manifeste la tendance générale et est dû au fait que la formation de divers maillons dans les chaînes d'alimentation d'Elton (1927) se produit non pas simultanément, mais successivement. Ce sont des liaisons

trophiques des phytophages avec la plante édificatrice, le blé, qui se forment en premier lieu, ces liaisons jouant le rôle de premier maillon dans les chaînes d'alimentation. Les maillons successifs–zoophage–phytophage et zoophage–zoophage–se forment après un certain temps. L'affaiblissement des barrières biologiques aux stades initiaux de formation des agrobiocoenoses, l'abondance de nourriture dans les champs, ainsi que le fait meme du changement de la plante de nourriture provoquant une augmentation de l'activité vitale de populations des oligophages nuisibles qui passent de l'alimentation en graminées sauvages dans la steppe à l'alimentation en plantes de blé dans les champs–tout cela contribue à l'accroissement du nombre de parasites des champs et crée des conditions pour la naissance d'invasion. Les conditions analogues sont créées dans les champs, lors de l'avancement des plantes cultivées dans de nouvelles régions de labourage, ainsi qu'après le traitement phytosanitaire effectué simultanément sur grandes surfaces.

Dans les conditions de la monoculture du blé, la succession naturelle et l'autorégulation qui se déroulent dans les agrobiocoenoses nonobstant les cycles agronomiques stabilisent nettement, au cours de 6-7 ans, la situation écologique. Le rôle des arthropodes parasites et rapaces croît d'une manière impressionnante tandis que le nombre d'oligophages nuisibles subit une nette diminution. Le niveau général de population diminue de 2 à 3 fois et s'approche du niveau de population propre aux champs labourés précédement.

Les traitements phytosanitaires massifs en rejetant la succession naturelle aux stades initiaux de formation de l'agrobiocoenose empêchent la manifestation de régulation naturelle et maintiennent la labilité de conditions dans les champs. Compte tenu d'adaptations des parasites des champs répandues dans ces lieux à la phénologie des graminées spontanées de steppe à longue période de végétation, il faut opposer à l'achèvement de leurs cycles vitaux une diminution des périodes de végétation du blé dans les champs par l'emploi des variétés précoces et des procédés appropriés de leur culture.

THE FORMATION OF PEST FAUNA BY AGRICULTURAL DEVELOPMENT IN NEW COUNTRIES

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Drastic environmental changes caused by agricultural development lead to complete reconstruction of the local insect fauna. Many species are eliminated but a few, favoured by the crops introduced, rapidly increase in numbers. The local fauna of wild plants related to crops is the initial reservoir of their pests and provides continuous replacement of losses inflicted by control within crops. Surveys of local wild fauna are necessary when development is planned.

THE IMPORTANCE OF ADJACENT UNCULTIVATED LAND IN RELATION TO CROP PEST INSECTS

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In Great Britain fields are normally small and mixed farming is a common practice. Thus crops normally form islands within larger areas of less cultivated land. Apart from the importance of uncultivated land as nesting sites for insectivorous birds, little is known of its importance with regard to insects although a search of the literature reveals many papers which mention the subject indirectly.

It seems possible to divide the relationship between uncultivated land and the insect fauna of a crop into two components:

(*a*) *Physical* (4) The shelter and shade caused by the height and density of the edge-growth may affect insects on the crop (sometimes indirectly *via* the plant) and those moved in air-currents. Many insects also seek the shelter and debris of a hedgerow for hibernation or aestivation.

(*b*) *Biological* The botanical components of uncultivated land (with the insect species they support) may have a place in the life-history and biology of insects found on the adjacent crop. Many insect pests feed on wild plants and may move on to the crop due to seasonal movements and irregular events such as the use of weedkillers on roadside verges. Such movements may result in the transmission of disease to the crop from wild hosts which are often symptomless. Similarly beneficial insects may utilise hosts on wild plants as alternate or alternative prey. Adult feeding at flowers is characteristic of many pests and beneficial insects prior to egg maturation.

By studying an infestation of cabbage aphid (*Brevicoryne brassicae* (L.)) on a sprout field bordered by dense trees and flowers along different edges, it has been possible to assess edge-growth effects quantitatively (1, 2, 3).

Early in the season immigrant alatae were deposited and found on the crop with reference to shelter and the initially higher edge populations were reduced by the invasion of coccinellids and anthocorids from the edgegrowth.

Aphids at the sheltered edge reproduced more slowly than aphids in the open parts of the field, so that–in spite of lower losses due to predators and dispersal–numbers at this edge remained low.

Syrphidae were the most important predators and their eggs were more numerous near flowers than at the centre of the crop or elsewhere at the open edge. Dissection of females showed that pollen feeding had taken place. Losses of aphids caused by predation could be linked with the observed predator distribution. Thus aphids at the open edges suffered most from predation.

Differences between crop areas in the proportion of colonies producing alate nymphs largely reflected the size and number of the colonies present. Reduction by dispersal of the numbers of aphids present in the areas tended to reduce the differences caused by heavier predation at the open edges. The distribution of aphid mummies due to parasitisation could not be correlated with edgegrowth factors.

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UNTERSUCHUNGEN ÜBER DIE DISPERSION UND ABUNDANZ VON BLATTLÄUSEN UND DEREN NATÜRLICHEN FEINDEN

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Die Untersuchungen werden im Rahmen von Arbeiten durchgeführt, die dem Aufbau eines integrierten Pflanzenschutzprogrammes gegen *Aphis fabae* Scop. in Samenrübenbeständen dienen. Wegen starker Schwankungen des Feindspektrums versuchen wir, dieses Ziel nicht durch systematische Variation eines Spritzplanes, sondern durch die Kausalanalyse des Massenwechsels von *A. fabae* zu erreichen (1, 5, 7).

Bei dieser Analyse konnten wir zunächst nachweisen, daß die natürlichen Feinde durchaus in der Lage sind, Massenvermehrungen von *A. fabae* zu unterdrücken (7). Experimentell bestätigte Modellüberlegungen lassen erkennen, daß der Massenwechsel als ein Wechselspiel zwischen der täglichen Vermehrungsrate der Blattlaus und der täglichen Vernichtungsrate der Feinde zu verstehen ist (4). Hieraus ergibt sich die Notwendigkeit, einerseits die Ursachen der Variabilität der Vermehrungsrate näher zu analysieren (7), andererseits das Zustandekommen der Feindwirkung zu untersuchen. Die Polyphagie der wichtigsten Feinde von *A. fabae* und deren lange Aktivitätszeit (Ende März bis Anfang November) sowie die relativ kurze Verweilzeit von *A. fabae* in Samenrübenbeständen erfordert neben der Feststellung der Fraßkapazität der einzelnen Feinde (2) eine Untersuchung der Wechselbeziehungen zwischen verschiedenen Standorten wie auch eine Erforschung der Orientierung der Feinde (3, 6, 8). Hier soll nur über die Wechselbeziehungen zwischen einzelnen Standorten berichtet werden.

Untersuchungen blattlausbesetzter Pflanzen ergeben in der Zeit von 1958-1963 an Kulturpflanzen und Unkräutern in allen Jahren ein Überwiegen der Syrphiden, während an Bäumen und Sträuchern der Anteil der einzelnen Feindgruppen beträchtlich schwankt. Bei Coccinelliden ist auffallend, daß ihr Anteil an Kulturpflanzen und Unkräutern nur dann hoch ist, wenn er auch an Bäumen/Sträuchern erhölht ist.

Prüft man, wieviel Prozent der blattlausbefallenen Pflanzen an den drei Standorten mit

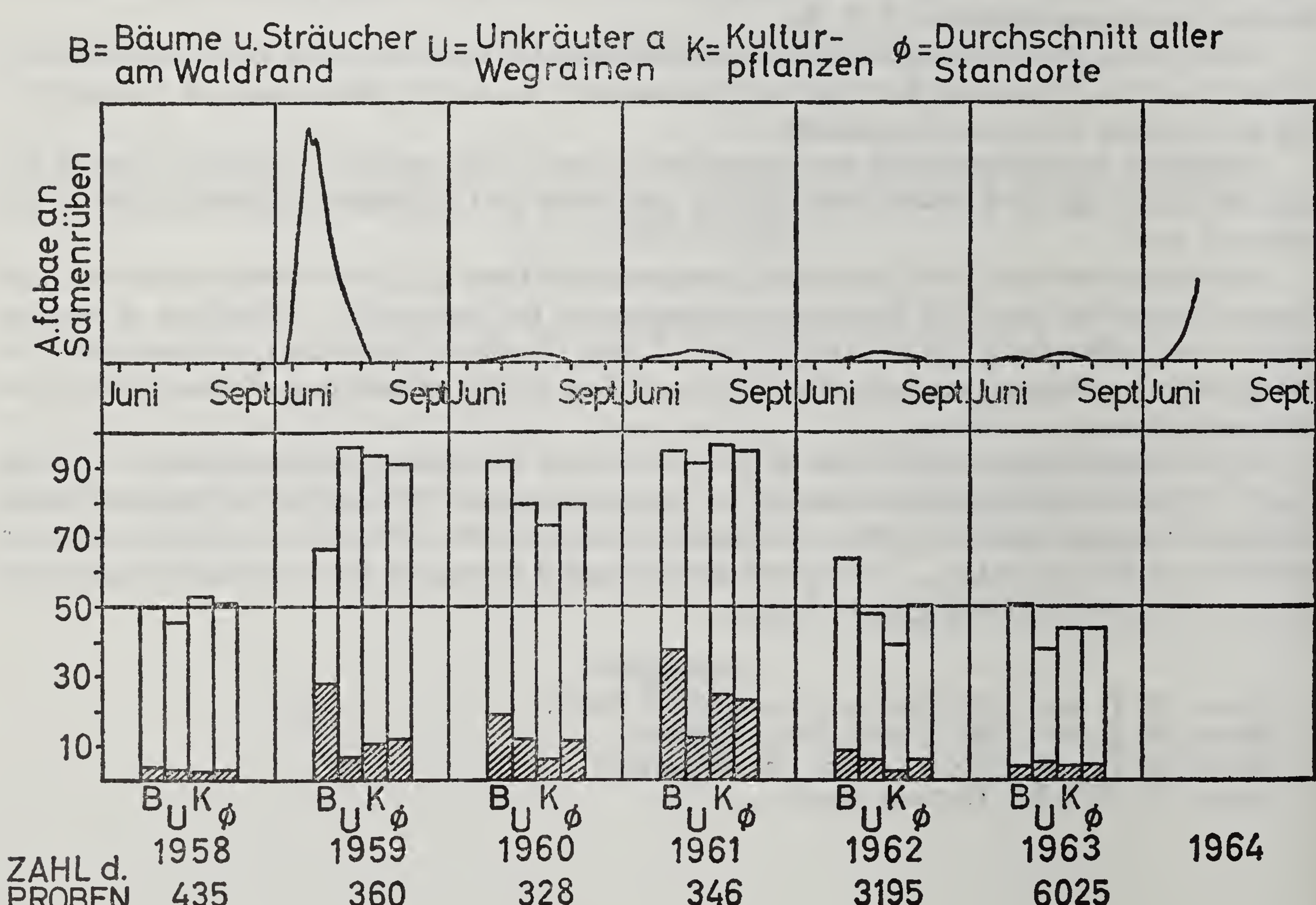

Abb. 1. Prozentsatz Blattlausproben mit Feinden sowie Dichte der Feinde an den Proben im Vergleich zur Vermehrung von *A. fabae*.

Feinden besetzt sind und wie hoch deren Dichte an diesen Pflanzen ist, so ergeben sich zwischen den einzelnen Jahren beachtliche Unterschiede. Auffallend ist, daß eine Massenvermehrung von *A. fabae* nur einem Jahr mit geringem Feindvorkommen zu folgen scheint (Abb. 1). Zur weiteren Überprüfung dieser Beziehung werden die Untersuchungen seit 1962 auf quantitativer Basis durchgeführt (Methode s. 5).

Verständlicherweise können diese Arbeiten wegen der Kürze der Zeit noch keinen Beitrag für die o.g. Beziehung liefern, jedoch lassen sie schon jetzt u.a. erkennen, daß mit zunehmender Besiedlung der Wegraine und Kulturfelder durch Blattläuse und deren Feinde ein Rückgang der Feinde an den Waldrändern einhergeht. Wie die Ergebnisse von 1962 andeuten, wandern die Feinde aus den Waldrändern in die offene Landschaft auch dann ab, wenn am Waldrand die Blattlausdichte weiter ansteigt.

Ein Vergleich der Blattlaus- und Feinddichte an verschiedenen Unkräutern läßt keine Korrelation zwischen den beiden Größen erkennen. 1963 ist eine zunehmende Blattlausdichte von *Potentilla spec.* über *Heracleum spec.*, *Sonchus spec.*, *Pastinaca spec.*, *Achillea millefolium* zu *Crepis spec.* festzustellen. Der Feindbesatz steigt dagegen von *Potentilla* über *Pastinaca*,

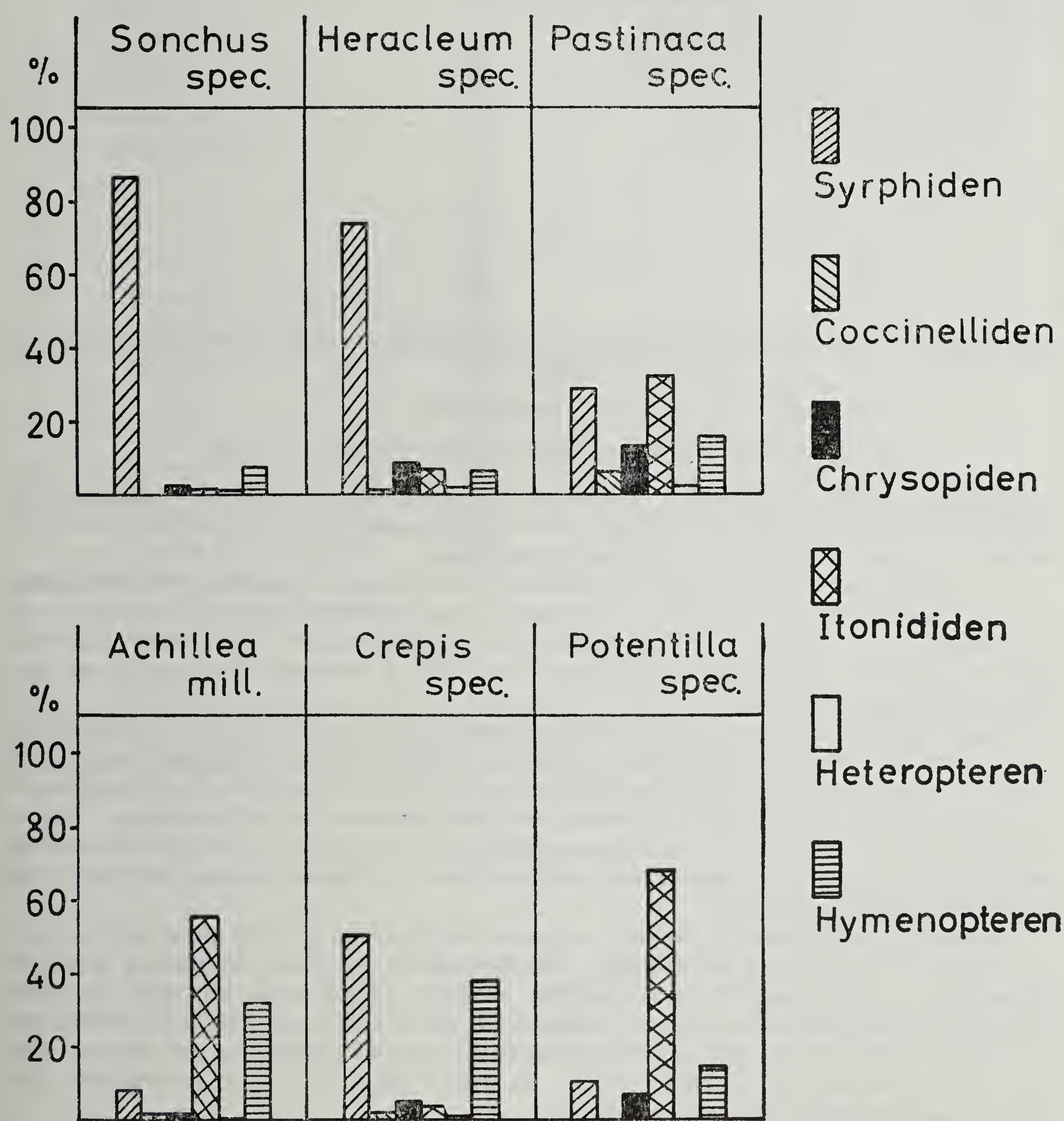

Abb. 2. Feindspektrum an verschiedenen Unkräutern (Jahresdurchschnitt).

Heracleum, Crepis, Achillea zu *Sonchus* an. Überraschend ist außerdem, daß an den genannten Unkräutern ein äußerst unterschiedliches Feindspektrum festzustellen ist (Abb. 2).

Diese Befunde deuten darauf hin, daß die Verteilung der Blattlausfeinde nicht nur durch das Auftreten von Blattläusen, sondern auch stark durch deren Wirtspflanzen bestimmt wird. Außerdem dürfte die Artzugehörigkeit der einzelnen Blattläuse eine wichtige Rolle spielen. Durch gleichsinnige Untersuchungen in den nächsten Jahren wollen wir prüfen, welchen Schwankungen die bisher gefundenen Ergebnisse unterliegen. Auf diese Weise hoffen wir, eine Basis für die Beurteilung von Pflanzengesellschaften in Bezug auf das Vorkommen von Blattlausfeinden zu erhalten bzw. eine Basis für eine bewußte Veränderung einer Vegetation zur Verbesserung der Lebensbedingungen von Blattlausfeinden zu erarbeiten. Außerdem hoffen wir Klarheit darüber zu erhalten, in welchem Umfang die oben angedeutete Beziehung zwischen dem Feindauftreten eines Jahres und der Vermehrung von *A. fabae* im kommenden Jahr Gültigkeit besitzt.

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THE PROGNOSIS OF THE SEASONAL APPEARANCE AND DEVELOPMENT OF INSECTS

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At present work on entomology, particulaıly chemical measures of combatting insects has broadened and become complex. Hence to carry out planned measures on a large scale it is necessary to possess a thorough entomological prognosis.

A complete prognosis clarifies the following four problems important for production:

(1) What kind of insects will it be necessary to take measures against? (2) Where,—in what districts? (3) When,—in what period? (4) To what extent? This paper deals with the third problem—phenological prognostication. This is necessary for carrying out any measures at the correct time.

As a basis of the phenological prognosis we make use of the rule of perennial phenodates persistence: Terrestrial insects appear in different phases of their development and in the greatest numbeı (bearing in mind the established periods of their development and appearance) at definite periods which change in different years and in certain limited boundaries. Therefore, for districts similar in their naturo-economic respect it is possible to establish the average perennial phenodates of the appearance and development of insects together with the extent of deviations from these dates".

First of all the average phenodates correspond to the climate in the given district, their deviations being dependent on weather. The phenodates aıe found by making graphical phenograms. The compiling of a calendar of insect development, but only for visual presentation, was proposed as early as the beginning of the past century by J. F. Judiech and H. Nitsche. We have improved and made use of this method for finishing phenological data during both research and production work. In view of this we had to create arbitrary signs (fig. 1), used for making phenograms (fig. 2).

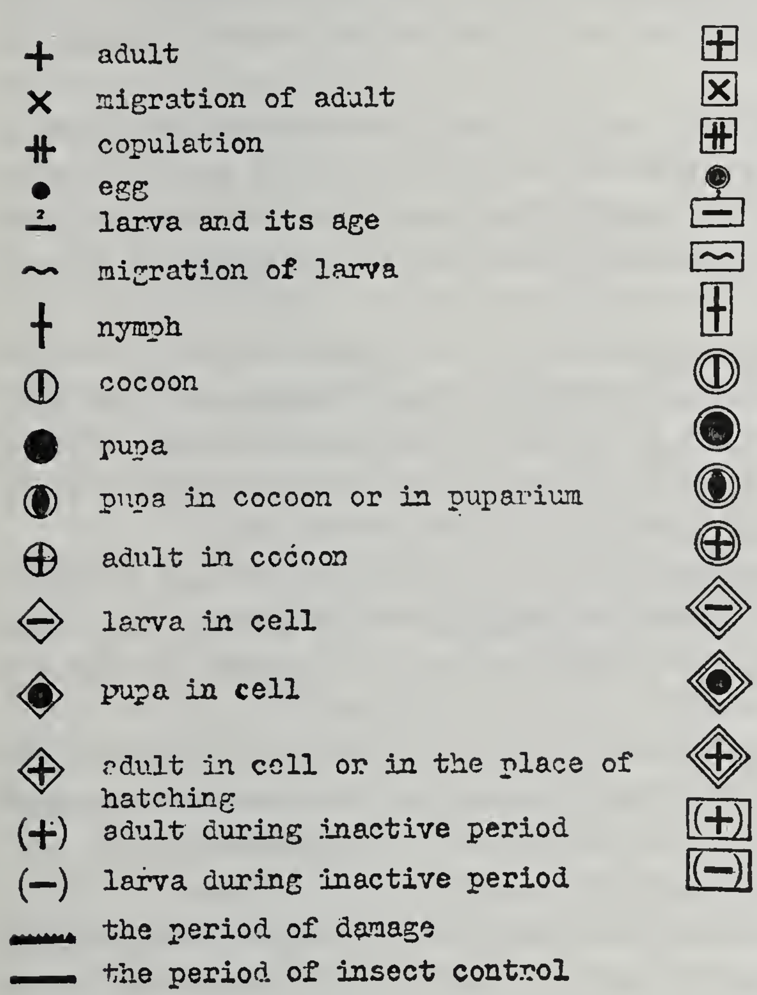
The phenological prognosis is made from phenograms compiled for regions having similar naturo-production characteristics. The annual prognosis is checked up during the

pre-spring period according to the prognosis of the forthcoming spring. Depending on the spring conditions and within perennial intervals the appearance and development of insects are shifted 10 days forward or backward. It has also been demonstrated that for making prognosis phenograms two or three year's phenological data are quite sufficient.

The phenogram method allows us to forecast a general time in a more or less exact way, and transfer all the annual entomological work on to a calendar basis. If necessary more exact methods are used of calculating time from data of insect development rate obtained under experimental conditions. For final commencement of work one uses coincidence together with the well pronounced phenological phenomena. Finally, use is made of observations in breeding cages both in laboratory and nature.

All these methods complement one another and are not at variance.

It seems advisable to set up an international system of phenological signs and that of making phenograms. The system described here has been adopted by the Board of Registration and Prognosis dealing with the protection of plants in the U.S.S.R.



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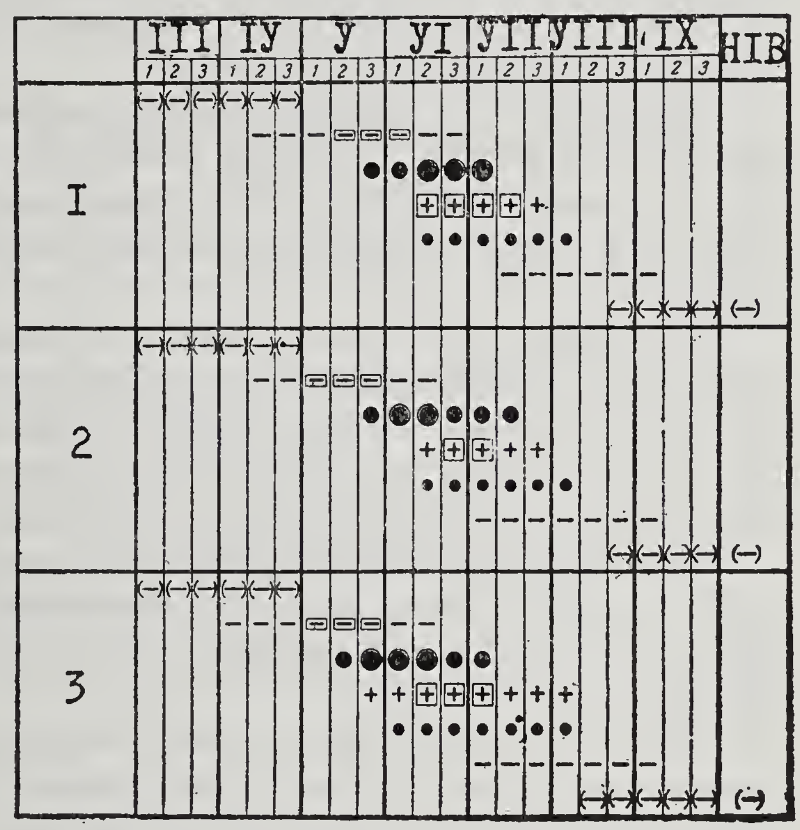

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Figs. 1, 2. (1) Arbitrary signs of insect phenology; method of encircling designates periods of maximum appearance. (2) Phenogram of the development of *Euproctis chryssorrhoea* L. in the North Caucasus: I Northern part, II Central part, III Southern part.

DYNAMIK DER VERÄNDERUNG IM BESTAND DER WICHTIGSTEN GRUPPEN KÄFER IN NATUR UND KULTURZÖNOSEN IN ASERBAIDSHAN UND DIE BEDEUTUNG DIESER VERÄNDERUNG FÜR DIE BILDUNG SCHÄDLICHER KOMPLEXE AN LANDWIRTSCHAFTLICHEN PFLANZEN

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Von den in der Fauna der Republik bekannten 2882 Arten Käfer, sind nur 431 Arten Schädlinge der landwirtschaftlichen Kulturen.

Die aussergewöhnlich komplizierten Ernährungsbeziehungen vieler Arten Käfer, die durch ihre unbeschränkte Ernährungsart gekennzeichnet sind erschweren nicht selten die genauere Bestimmung der Faunakomplexe einzelner Gruppen von Kulturpflanzen. Bei einer geringen Zahl Arten, die mit bestimmten einzelnen Pflanzen oder Pflanzengruppen biologisch verbunden sind, ist es dagegen möglich, die schädliche Fauna von Coleopteren dieser Pflanzen genau zu bestimmen.

Die Analyse der in dieser Richtung in Aserbaidshan ausgeführten Beobachtungen ergeben schroffe Unterschiede sowohl im Bestand der Arten der Faunenkomplexe, die auf einzelnen Pflanzen leben, als auch in der Abstufung ihrer Schädlichkeit und der wirtschaftlichen Bedeutung einiger Gruppen schädlicher Käfer in Abhängigkeit von den natürlichen Landschaften.

Es ist festgestellt, dass unter den obenerwähnten schädlichen Arten über 22% den Hauptbestand der Schädlinge an landwirtschaftlichen Kulturen bilden, von denen aber nur 8% beständig schaden. Zu den letzteren gehören solche typisch südliche Arten wie *Zabrus morio* Men., *Anisoplia leucaspis* Cast., *A. austriaca major* Reitt., *A. farraria* Er., *Polyphylla olivieri* Cast., *Pedinus femoralis volgensis* Müll., *Cerambyx dux* Fald. u.a.

Nebensächliche Schädlinge, die 62 Arten umfassen, kommen nicht oft vor und schaden nicht so stark, werden aber bei massenhaften Auftreten gefährlich und können Schaden anrichten. Als neue Schädlinge landwirtschaftlicher Pflanzen sind 18 Arten festgestellt worden.

Nach der Ernährungsart gehört die überwiegende Zahl der Käfer zu den nichtspezialisierten Polyphagen oder zu den weitunbeschränkten Oligophagen, die von der Gesamtzahl der schädlichen Käfer entsprechend 37,6 und 45,4% ausmachen; echte Monophagen und engbeschränkte Oligophagen kommen verhältnismässig selten vor.

Die Aufklärung der Ernährungsbeziehungen der schädlichen Käfer in den Verhältnissen natürlicher Zönosen ist von grosser Wichtigkeit nicht nur zur Bestimmung der Wege ihrer Verbreitung und der Grenzen ihres geographischen Areals, sondern auch zur Präzisierung der wirtschaftlichen Rolle der einzelnen Formen. In Aserbaidshan sind die am meisten spezialisierten Arten unter den schädlichen Käfern in natürlichen Zönosen auf folgenden Pflanzen beobachtet worden auf Rosaceae-103 Arten, auf Compositae-137, auf Cruziferae-129, auf Leguminosae-112, auf Gramineae-109 und auf Chenopodiaceae-84 Arten.

Der Bestand der faunistischen Gruppen der an einzelnen landwirtschaftlichen Pflanzen in Aserbaidshan schädigenden Käfer weist eine grosse Reichhaltigkeit Mannigfaltigkeit auf. Es muss aber betont werden, dass im Bestand der Ökologo-Faunistisch Komplexe der Käfer in Kulturzönosen ein nur geringer Prozentsatz des Übergangs aus der einheimischen wilden Fauna der wüstenartigen Steppen auf die Anbauflächen der Kulturpflanzen vorkommt, und die Fauna der letzteren keinen Wüstencharakter trägt, sondern eine mesophyle Gestalt mit einem Zusatz einzelner Arten halbwüstlicher Abstammung hat.

Die gewonnenen Ergebnisse erfordern ein komplexes biozönotisch Studium der Entomofauna der Kultur= und Neulandbiotope, das eine theoretische und praktische Bedeutung für das Verständnis der Bildung der Fauna der Agıobiozönosen hat.

EFFECTS OF MODERN AGROTECHNICAL METHODS ON THE AGRICULTURAL INSECT PEST POPULATIONS IN ISRAEL

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During the last 15 years, agriculture in Israel has experienced a period of transition from a primitive homestead type to mechanised modern farming, posing new problems in control of insects that had formerly been unknown as pests, or of little importance. The following examples illustrate this.

(1) Neglect of abandoned orchards and groves led to an increase of pest populations during the first years, chiefly borers in dead wood e.g. *Stromatium*, *Apate* (Buprestidae).

(2) Extension of existing cultures into hitherto uncultivated areas lead to an intrusion of insects from the surroundings. In the mountains, where new orchards are surrounded by macchia, *Prionus* attacked row after row of fruit trees causing their death, and *Apate* developed into a serious pest difficult to control.

(3) Introduction of new crops on large areas gives excellent possibilities for mass development by pests, formerly of minor importance e.g. *Prodenia*, *Laphygma*, *Chloridea*. Rice cultivation in the Huleh region was abandoned because of heavy attacks of *Chilotraea*.

(4) Irrigation of formerly unirrigated cultures lead to an increase of scale insect, aphid and mite populations. In cucurbitaceous crops *Epilachna* and *Baris* developed as pests.

(5) Extension of the growth season in irrigated cultures by staggered sowing or planting increased the number of generations of *Sesamia* from 2 to 3; the European cornborer became a pest in irrigated summer cereals only recently; the larvae of *Syringopais* emerge from their diapause in irrigated fields in August-September instead of December.

(6) Precocious sowing of melons retards germination in cool weather, and so the seeds are attacked by *Hylemyia cilicrura*, which will develop at 4°C. Plastic covers as a control measure, prevent the penetration of the fly and accelerate germination.

(7) Overhead irrigation encourages development of soil insects e.g. *Tenebrionidae*. Development of *Rhaphidopalpa* in cucurbit fields was formerly restricted to the walls of ditches as the eggs need contact water for development. Today they are able to develop all over the field, much nearer to the plants the roots of which they destroy.

(8) Green manure (chiefly *Lupinus*) and its ploughing under in March-April has lead in certain regions to an enormous increase in the tenebrionid populations, the larvae of which feast on decaying plant material and the adults of which then attack summer crops.

(9) In orchards in which the soil is not ploughed in spring to prevent excessive development of weeds, a substantial increase of *Lamellicornia* larvae (chiefly *Anoxia*, *Pentodon*) occurred.

(10) Thinning out of citrus groves from 4×4 m. to 4×8 m. distance between trees gives during the first years more light to the trees and leads to an increase of *Aonidiella* and *Ceroplastes* together with a reduction of *Chrysomphalus* populations.

Not all agrotechnical innovations have a deleterious effect. Deep ploughing considerably reduced the populations of *Syringopais* in barley fields and irrigation of stone fruit orchards prevents the development of *Capnodis* by killing the eggs which are very susceptible to high soil humidity.

Conclusions. As every insect pest can be controlled, chiefly by chemical means, introduction of new agrotechnical methods should not be prevented, but agronomists should consult applied entomologists prior to their introduction on a large scale, and calculate additional expenses for control, in the evaluation of new methods. It also should be pointed out, that insects may turn into pests only after several years of application of new methods.

DIE WIRKUNG VON INSEKTIZIDEN AUF EINIGE BEDEUTENDE TEILE DER FELDINSEKTENFAUNA

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Bei der Verwendung von nicht spezifischen Insektiziden—wie DDT und HCH, wird die gesamte order fast gesamte Entomofauna auf den behandelten Flächen beeinflusst. Durch Verwendung spezifischer Insektizide sind die Schäden viel kleiner, trotzdem werden auch die Prädatoren und Parasiten betroffen. Wir haben untersucht, welche Arten und in welchen Mengen je Flächeneinheiten bei der Behandlung gegen den Kartoffelkäfer getroffen werden und an Beispiel von Carabiden untersucht, wie sich ihre Zahl nach den Eingriffen erneuert. Im Labor haben wir den Einfluss einiger systemischer Insektizide auf die Prädatoren und Parasiten der *Aphis fabae* untersucht.

Bei der Kartoffelkäferbekämpfung wurden alle an den Feldern vorkommenden Insektenarten betroffen. Auf den Flächen von 100 m^2 waren z.B. 210-396 Dipteren, davon 20-34 Syrphiden, 72-203 Arachniden, 24-48 Carabiden, 13-41 Staphyliniden, 3-10 Vollkerfe und 13-38 Larven von Coccinelliden.

Auf Grund von in verschiedenen Perioden durchgeführten Versuchen über die Beeinflussung einzelner Arten der Lebensgemeinschaft der Kulturfelder haben wir ermittelt, dass die in der Literatur erwähnten unterschiedlichen Ergebnisse auf der Nichtberücksichtigung der Jahresperiodizität einzelner Arten beruhen. An den Carabidenarten *Pterostichus vulgaris* und *Harpalus rufipes* konnte gezeigt werden, dass binnen einer kurzer Zeitperiode völlig unterschiedliche Ergebnisse gewonnen wurden.

In Laborversuchen gewonnene Ergebnisse zeigten, dass die zur Vertilgung von Blattläusen und Rübenfliegen benutzten Insektizide eine sehr unterschiedliche Wirkung auf die Prädatoren und Parasiten ausüben. Von den drei untersuchten Insektiziden—Fosfotion, Intration und Soldep war am wirksamsten die Bespritzung, schwacher die Tiefenwirkung und am schwächsten die Kontaktwirkung. Fosfotion wirkt auf die natürlichen Feinde der Aphiden viel wirksamer als Intration, vom tiefwirkenden Soldep werden aber auch bei der Nahrungsaufnahme der behandelten Aphiden—die natürlichen Feinde der Aphiden beeinflusst.

Bei der Würdigung des Einflusses der Insektizide auf die Insektenfauna müssen wir stets von genauen Angaben über einzelne Arten, insbesondere von der Kenntnis ihres Jahresvorkommens, ausgehen. Obgleich sich die Angaben einiger Autoren voneinander völlig unterscheiden sind diese Ergebnisse richtig, gelten aber bloss für eine beschränkte Zeit und eine bestimmte geographische Lage. Wenn wir die Arbeiten betrachten, die die Einflüsse nach dem zahlenmässigen Stand ganzer Gruppen würdigen, müssen wir sagen, dass uns diese nur wenig Daten für eine wirkliche Wertung des Einflusses chemischer Eingriffe vermitteln.

Die nach dem Eingriff festgestellte Erneuerung der Entomofauna ist noch kein entscheidendes Kriterium für die Beurteilung, inwieweit der Eingriff in der ganzen Gemeinschaft wirksam wurde. Die Erneuerung tritt durch Änderungen in der Gesamtzusamensetzung der Fauna und durch Migration von Insekten auf die behandelte Fläche aus der Umgebung ein. Der Einfluss wird sich erst im darauffolgendem Jahr zeigen, weil ein Teil der Insekten keine neue Generation gründen konnte.

Unser Streben muss darauf hinauslaufen, die Insektizide so einzusetzen, dass ihr Eingriff die Schädlinge möglichst wirksam aber ökonomisch betrifft, dass aber die Lebensgemeinschaft möglichst wenig geschädigt wird. Der chemische Kampf gestaltet sich heute äusserst kompliziert und wir erblicken eine wesentliche Besserung in der "Biologisierung" des chem. Kampfes und Erhöhung der Qualifikation der Mitarbeiter des Pflanzenschutzes.

(4) EFFECTS OF AGRICULTURAL PRACTICE ON THE ECOLOGY OF PEST SPECIES

ECOLOGICAL ASPECTS OF CONTROL OF OLIVE SCALE, *PARLATORIA OLEAE* (COLVEE) BY NATURAL ENEMIES IN CALIFORNIA

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Since 1951 imported *Aphytis maculicornis* (Masi) has become a potent control agent of olive scale in California. Marked declines in the high densities of this pest have occurred. Huffaker *et al.* (1) appraised the results, ecologically and economically.

A. maculicornis is an ectoparasite that has a short life cycle in summer. Adults are intolerant of the hot dry summers and the short life cycle does not leave the parasite in the resistant immature stages long enough for it to "escape" the severest summer period.

This parasite is an efficient searcher even when hosts are scarce or when concealed beneath overlapping scales. Parasitisations of 90% in low host densities are common. It has a high increase rate. In the field it produces about five effective generations in the fall and spring. Increase is sometimes rapid in the fall, but this often starts from low levels; an appreciable density may not be attained until April or May. A "geometric" increase in the parasitisation from mid-March to mid-May usually occurs. During summer the generation time is less, but adults die quickly, producing few eggs. No effective multiplication occurs. Instead, sharp decimation proceeds from mid-June to about September.

In favorable locations summer parasitisation by *Aphytis* remains at 2 to 5 per cent and where good pruning, fertilisation and irrigation are practised this parasite alone has given control.

The control required is stringent. Crawlers concentrate on fruits. Largely because of summer severity on the parasite, full control has been too unreliable for general acceptance. *Aphytis*' performance varies with the year, location, and cultural conditions. Adverse summers are more severe on *Aphytis* than on the scale. Severity on the scale affects the rate of its increase during the summer when *Aphytis* pressure is low, and severity on the parasite, rendering the latter negligible in summer, also determines its recovery sufficiently early to curtail scale egg deposition by May. During milder summers scales and parasites survive better. This causes an *immediate* increase in scaly fruits (young scales), whereas the advantage of *Aphytis* only shows up commercially the following year! Nevertheless, great value from this parasite occurred all over California. It removed this scale as a major pest of shrubs, park and dooryard fruit and shade trees. By using a DDT "check-method" of removal of *Aphytis*, densities in olives increased from 100 to 900 times the levels where *Aphytis* was left unharmed.

The recently established *Coccophagoides* sp., has a powerful additive value, making sole reliance on *Aphytis* unnecessary. This species has a complex life cycle, females developing as primary endoparasites of *P. oleae* and males developing ectoparasitically on their own females. Its biology has been studied by Sarel Broodryk (unpublished) and the present authors.

Our present concern is the competitive dynamics of *Aphytis* and *Coccophagoides* in the control of olive scale. An additional parasite more tolerant of summer conditions which could effectively fill the almost unoccupied niche of utilising scales of the spring generation was obviously needed. Dr. Paul DeBach sent a shipment of *Coccophagoides*, undescribed, from Pakistan in 1957. This parasite appears to have the necessary attributes. Being an endoparasite and closely synchronised in its life-cycle to that of *P. oleae*, it spends the hottest period of summer as immatures protected from the summer severity.

Coccophagoides is also a good searcher and readily finds overlapped scales. Parasitisation is about 50 to 60% at host densities reduced below those when *Aphytis* was present alone.

Aphytis still holds its high level of efficiency in the spring. Until *Coccophagoides* approaches "mummification" of the host, *Aphytis* does not distinguish, but afterwards it does. When both parasites attack simultaneously *Aphytis* wins. *Aphytis* has 6-8 full or partial generations per year while *Coccophagoides* has only two basic, and two additional partial generations. *Coccophagoides* accepts small hosts; *Aphytis* does not—a security factor for *Coccophagoides* against *Aphytis*' higher power of increase.

Other things being equal, unless the winter and spring were more favorable to *Aphytis* than to such a summer-tolerant species, then *Coccophagoides* should supplant *Aphytis*, since the former would be present in greater numbers each fall. "Other things" favor *Aphytis*' rebound on the fall generation (spring period activity), and *Coccophagoides* dominates only on the spring generation (summer activity). Control since establishment of *Coccophagoides* is superior to that when only *Aphytis* was present.

In spring the indispensable parasitism by *Aphytis* is high and the species dominant, while the indispensable parasitism by *Coccophagoides* is low, a large portion of its parasitism being compensatory, causing deaths *Aphytis* would cause if *Coccophagoides* were not present. Much of the parasitism by both parasites is indispensable in the summer, but *Coccophagoides* is overwhelmingly dominant. During years less favorable to *Aphytis* the supplementing impact of *Coccophagoides*, even on the fall generation, would be more important and act as a strong reliability factor, as its summer activity does. Comparing parasitism by *Aphytis* on *Coccophagoides*-free hosts with its parasitism on *Coccophagoides*-parasitised hosts we estimated searching performance of *Aphytis*—its potential for destroying hosts parasitised by *Coccophagoides* if the latter were absent.

The data furnished estimates of the dispensable and indispensable fractions of *Coccophagoides*, parasitism. The full parasitism by *Coccophagoides* was used to estimate the dispensable and indispensable fractions of *Aphytis*' parasitism. This method was verified by comparison of two groups of 10 locations each where *Coccophagoides* is effective and where it is unestablished. In spring *Aphytis* performed uniformly as well on all the hosts where *Coccophagoides* was absent as it did on the *Coccophagoides*-free hosts only, in groves where the latter was effective. Parasitism by *Aphytis* was slightly higher where *Coccophagoides* was absent, but, the combined net parasitism was 88·2% while that by *Aphytis*, where present alone, was 83·6%.

The general parasitism in spring of neither species is correlated, or only very slightly, with combined net parasitisation, whereas the parasitism by *Aphytis* on *Coccophagoides*-free hosts is strongly correlated. The general parasitism by *Coccophagoides* is correlated with the indispensable fraction of this species' parasitism. An overlapping and mutually compensatory action of the two parasites is seen.

Tests using DDT for interfering (1) more with *Aphytis*, (2) more with *Coccophagoides*, (3) with both species, compared to (4) plots where both species were undisturbed, support conclusions that *Aphytis* is superior but that *Coccophagoides* adds a needed element of reliability; combined, a higher degree of control is maintained.

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DIE ENTWICKLUNGSABHÄNGIKEIT VON *QUADRASPIDIOTUS PERNICIOSUS* (COMST.) AN UMWELTFAKTOREN

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Im Rahmen des ökologischen Studiums der San José-Schildlaus (*Quadraspidiotus perniciosus* Comst.) erachten wir für notwendig die Einflüsse grosser Anzahl von Faktoren zu studieren. Dies sind die Einflüsse der abiotischen Faktoren und auch die Einflüsse des ganzen Komplexes von biotischen Faktoren und anthropogene Einflüsse. Die Temperatur zeigte sich unter Bedingungen in der Tschechoslowakei, nicht z.B. in Ungarn, als der führende Faktor für die Existenz und Schädlichkeit dieser Art.

Die Wärmeentwicklungskonstanten wurden in zahlreichen Expeıimenten festgesetst. Laborresultate wurden unter verschiedenen Klimabedingungen im Freilande beglaubigt. Der Wert des physiologischen Nullpunktes wurde mit 7,3°C, der Wert der Summe von Effektivtemperaturen, notwendig für die Entwicklung des ganzen Entwicklungszyklus, mit 770°C festgesetzt. Von 770°C fällt der Summe von Effektivtemperaturen, die für die Entwicklung der Erstlarve notwendig sind 200°C, für die Entwicklung der Zweitlarve auch 200°C und für die Entwicklung des Weibchens, incl. ihrer Embryen 370°C zu.

Es wurde festgestellt, dass in den nördlichen Gebirgsgebieten in der Slowakei keine Entwicklungsmöglichkeiten für die San José-Schildlaus bestehen. In den Vorgebirgslagen gibt es die Entwicklungsmöglichkeit nur für eine Generation und eine fakultative Entwicklungsmöglichkeit für zwei Generationen nur in warmen Jahren. In der Tiefebene der Südlslowakei sind weite Gebiete mit einer regelmässigen Entwicklungsmöglichkeit für zwei Generationen. In mehreren Versuchen wurde festgestellt, dass die Schildlaus in der Zone mit einer Generation, fakultativ mit zwei Generationen in der Slowakei unschädlich ist.

Im Südeuıopa scheint hohe Temperatur als markanter Regulationsfaktor zu sein. Die Temperatur von 35°C zeigte sich als die Obergrenze der Existenz unter Laborbedingungen. Konkrete Ausbreitung der San José-Schildlaus in Europa bestätigt diese Eıkenntnis. In den Gebieten, wo in Sommermonaten die Temperatur bis 35°C erreicht, ist die San José-Schildlaus wenig verbreitet und fast unschädlich. Europäische Gebiete mit einer theoretischen Entwicklungsmöglichkeit für 4 und mehrere Generationen sind durch diesen Schädling nicht bedroht.

Dies ist aber nicht für alle Weltkontinente gültig. Z.B. in Kalifornien kann die San José-Schildlaus bei 4-5 Generationen eine hohe Populationsdichte erreichen. Die Sommertemperaturen sind hier nicht höher als 30°C.

Laut unseren Versuchen ist auch die Diapause durch die Temperatur bedingt. Die Gleichung der Geraden, welche das Verhältnis der in der Diapause sich befindenden Tiere zu Temperaturbedingungen veranschaulicht, lautet: $y = -0{,}09x + 23{,}2$. Die Jungen, welche sich bei der Temperatur von 14,2°C und event. bei einer niedrigeren Temperatur entwickeln, kommen alle in die Diapause; jene Jungen, deren Entwicklung bei der Temperatur 23,2°C, event. noch höherer verläuft, entwickeln sich ohne durch die Diapause gestört zu werden.

Die Temperatur ist der führende Faktor in jenen Gebieten, die die Zonen, wo eine Entwicklungsmöglichkeit für zwei Generationen gegeben ist, umschliessen. Im Rahmen der Zweigenerationszone kommen in den Vordergrund andere Faktoren, z.B. in Ungarn, vorallem die Pflanzenresistenz und die natürlichen Feinde.

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ROLE OF NATURAL CAUSES AND CONTROL MEASURES IN THE DECLINE OF A MAJOR LOCUST PLAGUE

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Within the past decade, at least half a dozen countries have reported Desert Locust damage on un unprecedented scale, on several occasions reaching rates of millions of dollars per month; and *one of the largest Desert Locust swarms ever reported*, more than 40 km long, was unambiguously recorded by *radar photography* over Delhi as recently as July 1962. (Mazumdar *et al.*, Proc. WMO/FAO Seminar on meteorology and the Desert Locust —in press).

At the present time, on the other hand, the overall level of Desert Locust populations is lower than at *any time in the past 24 years*, with only *three reports of swarms*—two of them somewhat doubtful—since the beginning of 1964, as compared with hundreds of reports per week a few years ago.

For the fifty-odd countries concerned with the control of this elusive pest, the vital questions of how long this present locust situation is likely to continue, and of what should be done to prolong it further, pose in turn the question of *how the present situation has come about*, on which the types of data available and the lines of approach being followed in current work were illustrated.

In interpreting what is observed of the overall rise and fall of locust infestations it is necessary to attempt to take into account any available information on the effects of *natural mortality factors* (on which field investigations have been undertaken in a number of countries in recent years), together with what is known of the *scale* on which locusts are likely to have been *killed* in particular control campaigns, relative to the *scale* of the locust *infestations* which were attacked; series of field assessments have provided data on these last two points. An important lesson of the past is that Desert Locusts have been at a *very low level before*, under circumstances to which it can be shown that early attempts at locust control are unlikely to have made any appreciable contribution.

The total area subject to invasion by Desert Locust swarms is about 30 *million sq. kms.* of which at least a *million square kilometres* are subject to breeding by swarms in 50% or more of years. On several occasions, from 1960 onwards, an *important proportion* of the overall locust population appears to have been *concentrated by meteorological* factors into a relatively limited area, of the order of a *few tens of thousands of square kilometres*, in which recent developments in the technique and in the national and regional organisation of control had made possible control operations which in scale and nature are likely to have been *more* effective, *by several orders of magnitude*, than any control operations ever undertaken in these same areas up to a few years previously. An outline account was given of the locust and weather situations and the control campaigns in Mauritania/Senegal in the summer of 1960, and subsequently in the Souss valley in Morocco in the winter of 1960-61, which was followed by the complete disappearance of swarming populations from north-west and western Africa.

ON THE INFLUENCE OF HORTICULTURAL PRACTICES ON APPLE APHIDS

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Apple trees of a modern orchard differ fundamentally from those of former times. The period of growth was confined to spring in such sparingly fertilised standard trees, and ceased soon after their flowering. Growth similar to that in young trees, is now maintained until late summer by pruning and fertilising.

Among the apple pests that have recently increased in importance we find spider mites, leafrollers, and aphids—all arthropods whose development is favoured by modern methods of pruning and fertilising. To this factor should be added in some cases the cultivation of particularly susceptible varieties.

Information in the literature as to the susceptibility of different varieties of apple to aphids is comparatively rare (e.g. 2, 4) except in the case of the woolly aphid, *Eriosoma lanigerum* Hausm. We compared therefore the fecundity of apterae fundatrigeniae of *Aphis pomi* DeG. in single cultures on various root-stocks (EM I, EM II, EM IX) and varieties of apple (Jonathan, Cox Orange, Berlepsch), without observing any significant differences. On the other hand, we repeatedly observed evident differences between the varieties as to their infestation with *Aphis pomi* on root-stocks in nurseries in spring (6). The young larvae hatching from winter eggs appear not to find sufficient nourishment on the late budding EM XIII and consequently die, whereas on the earlier budding plants (for instance EM I, EM II) they survive far more easily. Great differences in infestation depending on the apple variety may be found in the field in the case of the red-gall *Dysaphis* species (*D. anthrisci* Börn., *D. chaerophylli* Börn., *D. radicola* Mordv., *D. brancoi* Börn.). Golden Delicious is extremely susceptible, often being the only variety in an orchard to be infested. Despite departure of migrants and the influence of predators colonies persist till the beginning of July. On other equally well-growing varieties of apple the colonies die out after the second generation in May, thus indicating varying possibilities of multiplication.

To investigate how growth conditions of the leaves affected the mortality and number of offspring of the apterae fundatrigeniae of *Aphis pomi* and *Dysaphis plantaginea* Pass. (Fierz, von Salis, Bürgi, not yet published), young larvae were placed singly in clip-on cages on young and old leaves. On old leaves mortality of such larvae is initially high. Insects surviving under these unfavourable conditions live as long, and in the case of *Aphis pomi* frequently even longer than the insects on young leaves. (cf. 1). The surviving females of both species produce an average of 50-90 larvae on young leaves, on old leaves the number of offspring is 60-90% lower. Similar tests weie conducted in the field. Here, too, analogous correlations were observed regarding mortality and fecundity.

Why young and old leaves as well as susceptible and resistant varieties differ in their suitability for aphids is still only partially known despite the many investigations being carried out (3, 5).

Results hitherto obtained make it evident why modern orchards present far more serious aphid problems than those of earlier times. The rosy apple aphid, *Dysaphis plantaginea*, and the red-gall *Dysaphis* species now find favourably growing shoots during their main period of development in May and June. The same applies even more to the green apple aphid, *Aphis pomi*, which invades the orchards in large numbers only in June.

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THE EFFECT OF SOIL INSECTICIDES ON THE NATURAL BALANCE OF THE CABBAGE ROOT FLY (*ERIOISCHIA BRASSICAE* BOUCHE)

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Since certain species of carabid and staphylinid beetles were first recognised as predators of the immature stages of the cabbage root fly, *Erioischia brassicae* (Bouché) (6, 7), investigations at Wellesbourne have shown them to be of considerable importance in the natural control of this pest. By using barriers to regulate the populations of carabids on plots of brassicae, Wright, Hughes and Worrall (1960) demonstrated that the numbers of root fly eggs and larvae were negatively correlated with the numbers of the representative species, *Bembidion lampros* (Herbst), trapped on the plots. In addition, Hughes (3) concluded that predation by *B. lampros* was the major cause of egg mortality during the first generation of the prey, accounting for over 90 per cent of the losses amongst the immature stages. Several species of carabids and staphylinids were identified as having fed on the immature stages in the field using an anti-cabbage root fly serum (1) and it was found that predation by staphylinids accounted for a greater loss of eggs and larvae than did the carabids present. *Aleochara bilineata* Gyll. and A. *bipustulata* (L.) were the commonest staphylinids found and amongst the carabids, *B. lampros* and *Harpalus aeneus* (F.) were the most frequently trapped species during the first generation of the fly and *H. rufipes* (Deg.) and *Feronia* spp. during the second. *Trechus quadristriatus* (Schr.) by reason of its behaviour (4) was not readily trapped in pitfalls but commonly found in the soil around the base of the plants from late June onwards. The combined predatory efficiency (product of the relative predatory value and abundance) was invariably greater and consequently more effective among the carabids trapped during the first than during the second root fly generation. This level of natural control, however, was never sufficient to reduce the numbers of surviving root fly to below pest status and the addition of an insecticidal control measure was necessary for maximum crop production. Efficient application of insecticides to the soil immediately around the base of the plants for root fly control, had little effect on the populations of predatory beetles, but when applied as a broadcast treatment their numbers were reduced. When the insecticide was applied in amounts insufficient to control the pest but high enough to affect the beetle populations a disturbance in the natural balance occurred. Laboratory and field experiments have indicated that the smaller species such as *B. lampros*, *T. quadristriatus* and *Aleochara* spp. were readily killed by quantities of dieldrin in the soil equivalent to 0·4 lb per acre, whereas the larger but less efficient predatory species e.g. *Harpalus* spp. and *Feronia* spp. were affected by amounts exceeding 1·7 lb. per acre. Such residue levels may occur in field soils following repeated commercial usage and can have a marked effect on the natural control of the cabbage root fly. This perhaps has been best demonstrated in situations where broadcast applications of insecticide have not only lead to a rapid development of resistance to cyclodiene insecticides in the cabbage root fly but have led also to a considerable reduction in the numbers of beneficial insects (2, 5).

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THE POTENTIAL SIGNIFICANCE OF *OULEMA MELANOPA* (L.), A RECENT INTRODUCTION TO NORTH AMERICA

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The chrysomelid, *Oulema melanopa* (L.), introduced into the United States of America at an inland location near Lake Michigan appears to be a grain insect pest of considerable magnitude. It was first recognised in 1962 by Professor G. E. Guyer of Michigan. The insect had been in the area for a minimum of four years prior to that time, and it is presumed to have come from Western Eurasia.

The 1962 records show only an area totalling 200 square miles in Michigan and Indiana. By the close of 1963, it had extended its range into Ohio with a total area of 18,000 square miles. Distribution records thru June 1964 indicate only a moderate geographical spread. The first focal point of infestation was Galien, Michigan, but the radius of high population density has increased markedly in the last 12 months. In northern Indiana, 10-15 miles from this area, the following increases were recorded:

TABLE 1
A comparison of early May populations of cereal leaf beetle adults infesting wheat prior to oats emergence with developing larval populations in oats in June 1963 and 1964

	1963	1964
Beetles per 100 sweeps	30·7	46·4
Larvae per 100 stems	169·7	327·7

Laboratory experiments measured the extent to which *O. melanopa* would feed and the amount of weight they gained. The beetles accepted barley (*Hordeum vulgare*), and rye (*Secale cereale*) more readily than oats (*Avena sativa*) or wheat (*Triticum vulgare*), but all four plants plus orchard grass (*Dactylis glomerata*) were preferred to corn maize (*Zea mays*), sorghum (*Sorghum vulgare*), millet (*Setaria italica*), and Sudan grass (*Sorghum vulgare sudanense*). Weight gain was best on oats, barley, wheat, and rye. Although orchard grass was readily consumed, the adults gained little weight from it.

Similar experiments conducted with larvae on a variety of plants indicated a high survival on barley, oats, wheat, and spelt (*T. spelta*); less on rye, orchard grass, and brome grass (*Bromus inermis*); and little to none on fescue, corn maize, sorghum, sudan grass, and millet.

In the field it is evident that young plants are preferred, and beetles feeding on overwintered wheat in early spring will move rapidly to oats when these plants first emerge from the ground, permitting recovery of the wheat. With respect to oats, however, research in 1963 showed losses in yield as high as 14 per cent from larval populations averaging one per stem.

Experiments are in progress utilising controlled climate programmed for other regions. The great acreages of spring planted wheat lie to the west of the present infestation of *O. melanopa* by 300 to 700 miles. It is now believed that the greatest impact of this beetle could be felt more in that region than in the Michigan-Indiana area. There, much of the wheat is planted in early spring and would be of ideal size to attract and support the overwintered adults.

The summer adults fly enough to be caught in updrafts of wind and carried to considerable heights. Specimens have been trapped repeatedly at 100 feet and as high as 1000 feet. Although the present program of parasite introduction may be successful, the fact remains that none are present in the west at this time to impede its spread.

This insect appears destined to be a mild economic problem in its present range, and there principally on oats, but it possesses the potential to disrupt not only oats, but also wheat and barley production in the northern areas west of 90° longitude.

THE CEREAL LEAF BEETLE, *OULEMA MELANOPA* (L.). A NEW INTRODUCED PEST IN MICHIGAN—BIOLOGY, ECOLOGY AND CONTROL

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The initial infestation of the cereal leaf beetle was identified from Berrien County, Michigan in June of 1962. Subsequently, surveys have indicated that at least 30 counties are infested in Michigan as well as large areas of Indiana and Ohio. How the cereal leaf beetle was introduced into Southwestern Michigan is still unknown.

The insect has one generation per year. They overwinter as adults. The overwintered adults are attracted to succulent grasses, particularly winter wheat and spring oats when they leave their overwintering sites in the early spring. Maximum larval activity occurs during the last of May and early June. Maximum adult emergence from the pupae takes place during the last week of June. The adults then feed extensively on green grains, succulent grasses, and young corn for approximately ten days. By late July, they have moved out of the grain fields and are found in the field borders or scattered through wood lots in cracks and other tight places.

Rearing has been accomplished in the laboratory at a temperature of 80°F, a relative humidity of 65% and a photoperiod of 16 hours. Rearing techniques are still not adequate for the production of large numbers of beetles. Special problems are involved with the manipulation of diapause and the mortality during the pupal stage.

The insect has been observed feeding on 34 gramineous hosts with most serious injury resulting to the succulent new growth of winter and spring seeded grains. Laboratory studies indicate that the adults will consume more than 140 times their own weight of leaf tissue during their feeding period and the larvae will devour more than 3 times their own weight per day.

The entire world collections of wheat, barley and oats including more than 38,000 individual selections are being evaluated for possible host plant resistance. There have been encouraging developments in the selective feeding on wheat with less resistance or tolerance evident in the oat and barley selections.

Insecticides have been evaluated in the laboratory followed by field studies of the more promising candidate materials. Under laboratory conditions, carbamates were generally the most effective, phosphates moderate and chlorinated hydrocarbons least effective. The larvae were more susceptible to the carbamates and phosphates than were the adults. The chlorinated hydrocarbons were equally effective against both adults and larvae. Under field conditions carbaryl, dieldrin, endrin, Guthion, lindane, and malathion provided high initial mortality. Carbaryl showed a strong ovicidal effect in the laboratory. Technical malathion applied from the air has been very effective against adult beetles at dosages as low as 3 ounces of actual toxicant per acre.

Gametogenesis and radioactive effects on reproductive tissues have been studied. It was found that the male beetles attained sexual maturity earlier than females. X-rays have produced completely inviable eggs at low dosages. The histopathological effects caused by radiation were degeneration of germarium, malformation, abnormal, and slow development of the oocytes.

These investigations are a result of the combined efforts of the entomologists and geneticists at Michigan State University and the United States Department of Agriculture.

THE CEREAL LEAF BEETLE, *OULEMA MELANOPA* (L.). REGULATORY ACTION AND ASSOCIATED SIDE-EFFECT STUDIES RESULTING FROM INSECTICIDAL TREATMENT

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The Cereal Leaf Beetle (*Oulema melanopa L.*) was first found in Berrien County, Michigan in 1962. Since that time an intensive survey and suppression program has been carried out. In 1963 some 41,600 acres were sprayed in spring and summer treatment. In 1964 some 49,000 acres were treated for adult control (spring) and 24,000 of these same areas were re-sprayed. An additional 45,000 acres was treated for the first time either for larval or summer adult control in 1964.

All insecticide spraying has been done cooperatively between the U.S. Department of Agriculture Plant Pest Control and the Michigan Department of Agriculture. Research on control, biology, and pesticide side effects has been performed jointly by the U.S.D.A Agricultural Research Service, Michigan State University and Purdue University. Quarantine regulations are promulgated by the U.S.D.A. and the several states.

This presentation deals with the efforts being made to monitor spray applications with particular reference to possible deleterious effects manifested as catastrophic decline or abundance of terrestrial and aquatic arthropods. Corollary studies are being carried out on possible deleterious effects on vertebrates. This paper is concerned chiefly with measurable effects on terrestrial and aquatic arthropods.

Replicated samplings were carried out on representative cover types and in the small water courses which characterize the Berrien County infestation. Findings were graphed and notes taken of deviations observed between treated and check areas. The aquatic fauna were catalogued to taxa commensurate with available resources; and indicator species compared between treated and check streams. Since a practical level of sampling intensity yielded great intra-plot variability, emphasis was placed on catastrophic decline.

In 1964 emphasis was again placed on documenting catastrophic decline of indigenous aquatic arthropods and on spectacular build-up of economic pests in forage crops. Some information is also being obtained on pesticide drift and residue persistence.

(5) INTEGRATED CONTROL

SOME ASPECTS OF BIOLOGICAL AND INTEGRATED CONTROL OF PESTS

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Integrated control of pests aims at the control of pests by coordinating the effect of natural enemies with the control through cultural measures and the use of physical means and chemical agents. First and foremost it tends to increase the inhibiting effect of the natural enemies on the multiplication of harmful organisms. Therefore integrated control first concentrates on the natural complex of resistance and tries to adapt the necessary physical, chemical or cultural measures to that complex. Integrated control essentially is a form of biological control.

The reason why the international working group on integrated control of the "Commission Internationale de Lutte Biologique contre les enemis des cultures" (C.I.L.B.) was founded, is that it was clearly realised that the exclusive chemical control often with a strongly preventive character, as it generally applied in practice nowadays, will not be able to provide the ultimate solution to the control problem.

One of the greatest drawbacks of chemical control is that it promotes the development of races of harmful organisms which are resistant against the most efficient chemical control agents. In many countries all over the world this problem is already present.

The solution of the control problem is sought in a harmonious coordination of biological, chemical and cultural control. An important feature of this *harmonising control* (2) is the integrated control in which adaptation and fitting of the chemical to the biological control is an essential point. Harmonising control includes also all measures which increase plant resistance or render it less suitable as a host.

The problem has two aspects, namely biological and chemical. The biological aspect is the more important since integrated control is conceivable only when the natural enemies have an important influence on the regulation of the population density of the harmful organism, that is to say in cases where they play an important role within the framework of biological control. If the natural enemies fail in this respect, then we need not think of integrated control.

It appears from literature that in a number of cases control could be exerted successfully along pure biological lines. Important results with biological control have been obtained in the tropics and subtropics as well as in the temperate zones, in island regions as well as on the continents, in cases where either the control of harmful organisms, imported from other regions was concerned, or where cases of discontinuous distribution of the most important natural enemies were involved. In both cases import of natural enemies of the harmful organism in its new habitat led to an effective control in a number of cases. However, also many failures are reported. In these cases recourse had to be made to other methods, which mostly resulted in chemical control or in a combined chemical and biological control.

Apart from the control of imported pests there is the control of autochthonous pests which developed historically together with the crop, having become an integral part of the fauna belonging to the crop. In such cases the significance of a predator or a parasite is not only determined by its relations to the pest-insect, but also the predators and parasites have their own enemies, which often become so numerous in the course of the season that they can temporarily almost eliminate the effect of the primary parasites or predators. The interrelations of the faunistic elements in fruit-orchards are studied by the members of the international working group on integrated control of the C.I.L.B. It appeared that in such old biocoenosis very complicated relations exist between hosts, predators, parasites and hyperparasites. The latter often hamper greatly the use of effective elements in biological control. However, we must know these relations before we are able to judge which is valuable and which is worthless, which should be spared and which is permissible to destroy.

The effect of the natural enemies can be increased by the following measures:

1. artificially augmenting their effect by mass-production in the laboratory and by liberating them in the field at the right moment;
2. importing useful species;
3. importing or selecting species or races, which are better adapted to the climate and the biotope;
4. selecting races of the natural enemies which are resistant to given control agents;
5. improving the possibilities for the development of the natural enemies in or in the surroundings of the plantations (among others by preparing places of refuge and of hibernation, by enriching the biocoenosis with certain plants, particular for the flower-visiting parasitic Hymenoptera or by maintaining elements in the vegetation which are foci of useful organisms);
6. cultural measures furthering the effect of natural enemies;
7. sparing useful elements by the choice of selective methods of chemical control. This point leads us to an ideal combination of biological and chemical control.

Integration of biological and chemical control places the curative (and not preventive) application of specific and therefore selective agents in the foreground. The chemicals with a wide range of activity—and among them especially those with a long residual action—will be applicable only in special cases.

In integrated control the application of pathogenic micro-organisms, in particular bacteria, fungi and viruses, may take an important place.

Past and current research has shown that the use of pathogens may be integrated with that of entomophagous insects, chemical insecticides and other control methods; however, the principal requirement is to discover "more and better" pathogens.

The classic example of autocidal control methods is the eradication of the screw-worm (*Cochliomyia homonivorax*) from the island of Curacao by the release of flies sterilized with gamma radiation. It promoted many studies to explore other possibilities for this method.

The development of chemical sterilants is still in the beginning. So is the work on the application of insect hormones as control agents, the work on sounds and other physical attractants to which only males react and the work on pheromones, sex-attractants, repellents and antifeeding compounds.

Integrated control requires quite a different attitude from the research worker and farmer than does chemical control.

In the case of integrated control the research worker has to study the biocoenosis of the biotope in which the noxious organisms live, to investigate the interrelations between its elements and to study carefully the sensitivity of the organisms composing the biocoenosis against chemical agents such as insecticides, acaricides, fungicides, and so on.

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PRACTICAL APPLICATION OF THE INTEGRATED CONTROL CONCEPT IN CALIFORNIA

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The literally unilateral use of insecticides against a variety of pests in California during recent years created secondary problems which at times bordered on disaster. Consequently the pest control philosophy has been largely revised towards one of integrated control.

Considerable progress has been made in the development of selective chemical controls. The greatest success has occurred in alfalfa where essentially all materials included in the official insect control recommendations have been chosen because of their experimentally demonstrated selectivity.

Substantial progress has also been made in integrated control in other crops. One of the most strikingly successful programs has involved cyclamen mite, *Steneotarsonemus pallidus* (Banks) in strawberries. W. W. Allen following the lead of Huffaker and Kennett (2, 3) carried out an intensified search for a selective acaricide that might be adopted for use against the cyclamen mite. His experiments led him to Thiodan, a material of high toxicity to *S. pallidus* but of only

moderate detriment to its predators (1). The results have been spectacular. Cyclamen mite once a devastating pest has subsided to only a modicum of its former seriousness. Correlated with this has been a reduction in costs and an increase in strawberry yields (W. W. Allen, unpublished data).

Considerable integrated control activity has been carried out in cotton. As a result several selective materials have replaced broadly toxic insecticides. Amongst these, Dylox (Dipterex), which was largely developed for cotton insect control by H. T. Reynolds, has had wide acceptance in the field. Currently polyhedral virus and *Bacillus thuringiensis* Berliner are under intensive investigation as potential selective controls for *Heliothis zea* (Boddie).

Recently Shorey and Hale (4) developed an effective selective control for *Myzus persicae* Sulz. in peppers. These workers found Thiodan (Endosulfan) to be relatively harmless to the aphids' natural enemies and this material has supplanted the broad spectrum materials as the recommended control.

Investigations on integrated control of grape pests are now also underway in California with particular emphasis on the grape leaf hopper, *Erythroneura elegantula* Osborne. This work coordinated by R. L. Doutt, is being carried out under a multiple approach. Thus selective controls are being sought, economic thresholds reevaluated, timing of treatments reassessed, and ecological manipulations attempted.

Although the program is only in its early stage of development, certain of its phases have already been implemented. For instance, in Tulare County, a key grape growing area, substitution of Thiodan for more broadly toxic phosphate materials has already brought about significant reduction in insecticidal treatments. (Personal communication from F. L. Jensen, Farm Advisor, Tulare County, California).

The programs just described represent the most advanced situations in California as regards integrated control of agricultural pests. In practice much of the screening of new insecticides now routinely includes testing of their effects on entomophagous insects. Thus the search for materials adapted to integrated control through selectivity has literally become a matter of policy.

Our efforts to exploit cultural practices or ecological changes which might enhance integrated control are still largely in their developmental stages.

However, considerable progress has been made in one of these programs, that involving the strip harvesting of alfalfa. Under strip harvesting, even at mowing time, half the field contains standing alfalfa. In this way the field becomes a relatively stable environment, rather than one which passes through catastrophic upset at each alfalfa harvest.

The strip cutting program has the dual objective of, (a) improving the balance of insect populations in the alfalfa fields thereby enhancing biological control of pests directly affecting the crop and (b) the prevention of migrations of the dangerous pest *Lygus hesperus* Knight from alfalfa where it does negligible damage to more susceptible crops. Preliminary studies conducted during 1963 indicated that these objectives of strip cutting may well be attained (5).

Discussion. The cases of integrated control just discussed fall far short of the full perfection of scientific pest control. However, they represent a major step in the right direction and they serve as an inspiration for the development of more sophisticated programs.

The programs already in effect or under intensive development occur in about one third of California's crops as based on dollar valuation. Thus it is evident that the integrated control philosophy is deeply entrenched and spreading rapidly amongst pest control researchers in the state.

Grower enthusiasm for integrated control has not been as high as with the entomologists. Though many growers have accepted the philosophy the bulk still prefer the broadly toxic materials which they feel will give them pest free and abundant crops. This attitude has slowed the rate at which integrated control programs are being adopted in California.

Another stumbling block to broadened adoption of integrated control lies in the fundamental nature of pest control advisement in the state. This advisement comes largely from the representatives of agricultural chemical companies or pest control services which sell or apply chemicals. There are hundreds of these company representatives in the state and quite probably they have by far the greatest influence of any group or agency over pest control measures actually put to practice on the farm.

Under this system scientific pest control is far from a reality and indeed at times takes on more of the aura of an insecticidal sales contest than that of a highly developed technology.

This situation is not favorable for the rapid and widespread acceptance of integrated control. However, there is little likelihood that it will soon change, since there is no wide scale truly scientific pest control system available to replace it.

It would seem that as the researchers develop more sophisticated integrated controls the only possible way that these programs can be widely implemented will be through the medium of highly competent independently operating professional entomologists.

Thus in California we stand at a critical mile post in integrated control where, depending upon the turn of events, it will either remain at its present level based largely on the selective use of insecticides or where through the medium of an evolving corps of independent agricultural technologists it will advance into its truly scientific era.

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TWENTY YEARS' EXPERIENCE WITH INTEGRATED CONTROL PROGRAMMES IN NOVA SCOTIA APPLE AND PEAR ORCHARDS

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Investigations on integrated insect control programmes in apple and pear orchards have been carried on in Nova Scotia for the past 20 years. The authors define integrated control as a programme of arthropod population management designed to keep pest populations below economic tolerance levels by maximizing environmental resistance and supplementing this by the use of selective pesticide applications if economic tolerance levels are threatened. The Nova Scotia programme which is dynamic in nature has been adopted on over 80 per cent of the apple and pear acreage.

The programme has evolved largely as a result of observation, experimentation, and trial and error, and has been predicated on achieving the maximum effectiveness of the natural control agents already established in the ecosystem rather than through their introduction or dissemination. It is evident that the area was reasonably well supplied with biological control agents which is probably a marked contrast to some other areas. This should not be construed as suggesting that conditions in Nova Scotia are unique, nor that agents responsible for maintaining a high degree of environmental resistance cannot be established in areas where they were originally present in only small numbers or were absent.

Orchard surveys have shown that as the acreage included in the integrated programme has increased damage from pests has decreased. Whether or not this is a function of time or the extent of the area or of a combination of the two is not clear. Area does appear to be an important factor, especially with highly mobile species, and attempts to establish integrated control programmes on small acreages will usually fail unless the pest species involved have strictly limited movements, such as that usually found in mites and scale insects.

Selective pesticides used include a number of fungicides—captan, cyprex, and glyodin being the most popular. These are used freely for the control of apple and pear scab. Insecticides include nicotine sulphate, ryania and lead arsenate. Some of the broad spectrum pesticides are used at times for certain pests but usually at much reduced dosages, or the materials are applied at such times that beneficial species will not be seriously affected. Phytophagous mites cause no appreciable damage under properly functioning integrated control programmes.

Cost records for insecticides for 1961 and 1962 on seven orchards with a combined production of 332,000 bushels show the cost per bushel at 2·5 cents. Fungicide costs averaged 5·5 cents per bushel in these orchards, making a total of 8 cents per bushel for spray chemicals as compared to 18 cents per bushel average in 1947-48-49 when a full insecticide programme was being used.

CONDITIONS OF MANAGEMENT OF TWO ORCHARD PESTS, ONE EXOTIC AND THE OTHER NATIVE TO SOUTH-EASTERN AUSTRALIA

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Codling moth is the most important insect pest of pome fruits in S.-E. Australia. Frequent applications of broad-spectrum insecticides are used to control it. This practice appears to have caused some increase in the injuriousness of other, previously less important pests, notably of *Epiphyas postvittana* (Walk,), the light-brown apple moth (LBAM). The ecology of both species was studied with a view firstly to understanding their population dynamics, and ultimately to improving current conditions of orchard pest control.

Codling moth, an exotic species in Australia, was found to increase under natural conditions virtually to the limit of its supply of larval food, i.e. fruits, each season. The densities of its populations are stabilised by mechanisms involving competition for larval food and competition for cocoon shelter. The rates of potential increase in seasonal populations are high, i.e. at least 70 larval entries into fruits for every individual surviving the previous winter, in the absence of intraspecific stress but including average effects of other limiting agents in the field. Under those conditions, the containment of codling moth densities at commercially acceptable levels—i.e. well below those at which intraspecific competition becomes operative—can be achieved solely through agents capable of causing very severe mortality in sparse populations. The only agents found adequate so far in that respect are insecticidal toxicants.

LBAM is a native, extremely polyphagous species. Its numbers tend to increase on fruit trees during the summer when the foliage of its evergreen hosts becomes unfavourable as food in the absence of new growth. Crowding on the tips of orchard trees can cause larvae to disperse and to feed on the surface of fruits, producing at times very heavy losses. Under natural conditions, infestations of LBAM are normally light to very light. Numbers are contained far below those which the actual availability of food and shelter could support on both wild and cultivated host plants. This was found to result from the combined action of a wide array of predators and parasites, supplemented in certain circumstances by that of at least one pathogen. It was established that the disturbances which spray chemicals caused in the arthropod fauna of orchards were a major factor in the occurrence of damaging infestations of LBAM on fruit crops. The rational management of the species implies therefore conserving its natural enemies.

Consequently, a system of protection against codling moth was devised and successfully tested, which consisted of minimizing the availability of shelter for overwintering cocoons (sanitation and malathion lacquer bands) and of supplementing the reduction in numbers thus achieved by suppressive spraying early in the active season with a relatively specific toxicant (ryania). Infestation by LBAM remained commercially acceptable. Field experiments showed moreover that damaging increases of LBAM could be detected in advance, and prevented by well-timed applications of *Bacillus thuringiensis*.

Publication of the detailed results of this research has begun in the Australian Journal of Zoology.

CONTRIBUTION TO THE PROBLEM OF INTEGRATED CONTROL IN APPLE ORCHARDS

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We began our researches by taking samples of insects and spiders. Then we examined the population density of the various species for one year (3) and possible fluctuations of this density in the course of several years. Since 1954 we have been testing the effects of some pesticides (7) and spray programs (2) on the ecosystem of apple trees. Today we work with integrated control on an area of about 75 acres and have to face difficulties that we did not meet with while experimenting on smaller plots.

In all our experiments a certain technique has turned out not altogether unimportant, a technique which I have called "Klopfmethode"—that is to say—the old and rather simple method of rapping or shaking the branches (6). To detect very fast-sitting or hidden animals however, this technique has to be completed by more appropriate methods, such as counting the animals on inflorescences or young shoots periodically or studying the population density of spider mites by means of the imprint method (1).

The first basic requirements for the application of integrated control is to know the respective condition of the fauna throughout the year. The "Klopfmethode" provides this information in a very short time. The adviser will then be able to determine at once which treatment is advisable and which insecticide should be chosen (5).

Another basic requirement for any application of the integrated control is to know exactly the effects of the various chemicals at our disposal. To find the general effect of a pesticide, between one test and another three days later, the killed or injured animals are collected in funnels beneath the top of the tree. A comparison with a parathion-treated tree and with an untreated one will thus show the differences of speed and width by which the respective chemicals effect the fauna.

In our attempts to dispense with phosphorus compounds we had to realise that there are only very few chemicals that can be used instead (4). To control the codling moth e.g., of all the usual pesticides only two will remain, namely DDT and Sevin. It is well known, however, that both chemicals stimulate the growth of the fruit tree spider mite. We cannot change this by adding an acaricide in order to render an application possible. In case we want to do without those two chemicals mentioned above there only remains the expensive Ryania and—as a biological control—*Trichogramma* or, against the various species of caterpillars *Bacillus thuringiensis*. In addition, we use the relatively selective Isolan against the aphids and Thiodan against all other pests. Thiodan however is selective only to bees.

It is obvious that, as a single supervisor cannot possibly inspect the whole area regularly, some pests may increase unnoticed to such an extent that economic damage will arise. This is particularly dangerous if the microclimate and the soil of the orchard in question differ considerably or if different varieties of apple trees are cultivated in no regular pattern. We were forced to limit the integrated control plot to a modernised part of the orchard, which covers an area of about 25 acres. There the trees are planted in larger plots of one kind only, by which fact the control and—if necessary—a partial treatment is rendered much easier. These experiences clearly refute any theory to the effect that an integrated control is advisable only for extensive fruit growing. On the contrary, this method of control turns out a full success in intensive orchards only.

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LES VOIES DE L'ENRICHISSEMENT DES AGROBIOCOENOSES D'ORGANISMES UTILES

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Dans les biocoenoses naturelles la composition et le nombre total d'espèces dependent de la mesure, dans laquelle sont satisfaites les exigences des espèces dominantes et constantes envers le milleu externe et de leur capacité de survivre dans la lutte interspecifique.

Le règlage de relations entre les espèces nuisibles et utiles, la saturation des biocoenoses d'organismes utiles sont le plus accesibles dans les agrobiocoenoses car elles sont formés d'une multitude d'individus appartenant a une quantité très restreinte d'espèces dominantes et constantes d'insectes nuisibles; leur composition vegetale est limitée.

On etudie des methodes d'enrichissement des agrobiocoenoses differentes:

l'implantation des nouveaux organismes utiles, création des conditions favorisant leur accumulation naturelle et leur conservation lors de l'application des insecticides.

On a argumenté les methodes d'affriandation des entomophages dans les agrobiocoenoses par l'introduction d'un composant complémentaire—plantes mellifères et trouve assortiment pour l'utilisation pratique. La parasitation des insectes nuisibles atteint alors 60-95%.

En URSS on a reussi la naturalisation d'entomophages specialisés, éprouvées a l'étranger, qui s'adaptent au climat local et survivent dans la lutte interspecifique avec les aborigènes des agrobiocoenoses.

Lors de l'application des poisons dans les biocoenoses des troubles considerables des relations interspecifiques ont lieu. De frequents traitments chimiques contre les espèces dominantes, destruisent les entomophages specialisés de complexe des insectes nuisibles; cela provoque leur reproduction massive. L'extermination des parasites polyphages, attaquant les insectes nuisibles eventuellement et sporadiquement, influence peut leur balance. L'action des poisons modifie aussi les relations internes des parasites avec leurs hôtes dans l'ontogenèse.

La resistance des larves parasitaires contre les poisons depend de leur age et de l'état de l'organisme de l'hote. Les plus resistantes sont les larves adultes des parasites qui se nourissent des tissus adipeux de l'hôte, formant une barrière lipeuse contre les poisons. Ces larves isolent aussi un secret conservant les tissus de l'hôte, affaiblissant et neutralisant l'action des poisons. Les jeunes larves qui se nourissent d'hemolymphe des chenilles par laquelle le poison se repand dans l'organisme de l'hôte ne sont pas resistantes.

La rationalisation de la lutte chimique consiste a determiner le delais et la frequence d'application, les preparations utilisés, leur formes, dosages—les plus favorables pour les entomophages; les traitements par bandes alternantes; applications de microorganismes combinées avec les petites doses des poisons; des poisons avec des engrais extra racines.

L'étape importante de l'enrichissement des agrobiocoenoses, c'est l'application combinée des entomophages et des microorganismes sur la même culture contre differents insectes nuisibles.

Au moyen d'utilisation combinée de *Trichogramma* spp. de biopreparation entobacterine et des plantes mellifères, on a parvenu pendant trois a reduire dans les expérience le nombre d'insectes nuisibles des choux à 70-98% et a proteger les recoltes; dans les régions d'une seule génération de *Carpocapsa pomonella* L. le degât s'est trois fois reduit; la récolte des pommes intactes a augmenté de 10-18 quintaux par hectare.

Pour nombre d'espèces on a constaté que l'immunité des chenilles contre les parasites oligophages diminue ou disparait sous l'influènce de petites doses des preparations bacterielles.

Toutes ces methodes permettent d'aborder le problème de l'augmentation de l'efficacité des organismes utiles dans les agrobiocoenoses et du remplacement pour certaines conditions des traitements chimiques par la lutte biologique.

BIOLOGICAL, MICROBIOLOGICAL AND CHEMICAL CONTROL OF THE PLUM MOTH (*LASPEYRESIA FUNEBRANA* TR.) (LEP., TORTRICIDAE) IN POLAND

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Experiments carried out in 1963 were a continuation of those carried out in previous years. Their aim was to compare biological, microbiological and chemical control methods against plum moth. An orchard was chosen containing more than 6,000 trees, 15 years old and practically all of the variety "Sweet prune". Each experimental group contained 100 trees, separated by isolation bands of 50 trees. Data was collected from 5-6 trees in each group including parasitisation of eggs and damage to fruits.

There were 18 groups as follows:—(1 and 2) Controls; (3) *Trichogramma cacoeciae* March. 2,000,000 individuals per 100 trees; (4) *T. cacoeciae*, 100,000 per 100 trees; (5) Bactospeine 0·25%; (6) Entobacterin 0·5% + Lebaycid 0·015%; (7) Boverin 3 kg/ha.; (8) Azofos 0·3%; (9) Azofos 0·1%; (10) Lebaycid 0·15%; (11) Anthio 0·2%; (12) Metox 0·5%; (13) Metox 1%; (14-18) *T. cacoeciae*, 500,000 per 100 trees, followed by Boverin, Bactospeine, Metox 0·5%, Metox 1% and Azofos 0·1% respectively.

Trichogramma proved to be the most effective of the biological factors, when used at the rate of 2,000,000 per 100 trees. It proved statistically better than micro-organisms and all chemical preparations with the exception of Azofos. Even when the numbers of *Trichogramma* were reduced by 20 times this did not result in any great changes in its effectiveness. When 100,000 individuals per 100 trees were used, results were obtained which were significantly inferior only to Azofos, but not less effective than the remaining combinations. Of the chemical preparations the best proved to be Azofos, which is more effective than micro-organisms, and better than Metox and Anthio. Preparations containing bacteria are, in general, fairly effective, although they are inferior to some chemical preparations in respect of absolute effectiveness. This is compensated for by the fact that these are the only safe and selective means hitherto in use. Of the mixed combinations, the best results were obtained on plots with *Trichogramma* and Azofos, and with *Trichogramma* and bacteria. It must, however be emphasised that even the best of these did not yield better results than those obtained by the use of *Trichogramma* and Azofos separately.

THE ROLE OF PATHOGENS IN BALANCED OR INTEGRATED INSECT CONTROL PROGRAMS

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For purposes of this discussion, a balanced insect control program has as an objective the establishment of host-parasite homeostasis in a particular environment. We are essentially concerned with those situations where an insect has been introduced into a new environment without a full complement of its natural enemies. Often we subjectively label as a "pest" this insect living at man's expense. The economics of the crop, value per area, or cost and availability of pathogens, will determine the choice of the balanced control procedure. In achieving a balanced control, a *single introduction* of a microbial pathogen may be sufficient to establish an enzootic, thus a focus or foci for subsequent epizootics. The microbial pathogen may be one of a number of beneficial organisms brought into a harmonious, balanced, natural state with other biotic factors in the habitat of the pest species.

Three elements characterise the use of pathogens in a "balanced" procedure:

(*a*) a single introduction at a selected point in space and time;
(*b*) periodic abundance of the pest in cyclical epizootics;
(*c*) *in vivo* propagation in the field or sustained saprophytically;
(*d*) evolution of host-parasite homeostasis in the ecosystem.

The evolution of homeostasis is of cardinal importance to the epizootiology of a disease in balanced or harmonious control, ensuring the effectiveness of the disease in frequent epizootics.

The balanced approach to control does not incorporate chemical insecticides in the procedure. This is a classical concept of biological control.

The introduction of a pathogenic virus into populations of lepidopterous and hymenopterous pests of large forested areas; or the introduction of a fungus pathogen into larval mosquito populations, are two examples of balanced control.

In contrast, the integrated insect control procedures would attempt to achieve an imbalance of the host-parasite relationship to the benefit of the crop and man. Economic loss in materials and time (i.e., food, fiber, or health) is avoided at the expense of *both* host and pathogen.

Characteristics of the role of pathogens in an "integrated" control procedure are:

(*a*) repeated introduction (or inundation by beneficial organisms (1)). Pathogen use is similar to that of chemical agents;

(*b*) no periodic abundance of pests, hence no crop damage or presence of disease vectors;

(*c*) opportunity for evolution to homeostasis of pathogen and host avoided by rotation of pathogens, various combinations and sequences of pathogens, or pathogen and chemical in combined applications.

If indeed we contrast the balanced and integrated procedures for pest control with respect to a selected insect pathogen, an important difference is evident: the *abundance* of the materials available for use in the control program. Can we conceive of a project to achieve a balanced control, supported by public or private funds that would provide sufficient inoculum of an insect pathogen for a single application over the entire range of a noxious insect?

The integrated control procedure draws upon pathogens as candidates for seasonal or repeated use in situations where the target insect and its host, plant or animal, is present for a limited time and in a restricted, generally cultivated area. For the balanced control procedure a single application is required on an enormous area. On the one hand we may have exclusive use of a biological control, on the other, use only as one factor in control or population management.

Those organisations capable of devoting a major effort to providing quantities of insect pathogens appear to be limiting themselves to a small fraction of the numerous insect pathogen candidates of significant potential. A count reveals 4 or 5 production processes patented in 6 or 7 countries for 2 organisms, *Bacillus thuringiensis* and *Beauveria bassiana* (2).

Investment of capital by public and private organisations appears to be in products for the short-term, integrated control procedure. Why should this be the case? Surely the prospect of providing for a single treatment of sub-continental areas of forest is as inviting as frequent, limited use of a pathogen!

What is the role of insect pathogens? Discussions on balanced and integrated control with insect pathogens presupposes the existence of agents that are effective. If the biological agents are not present or available in quantity we have little with which to work.

In addition to public institutions, we must expect to have industrial participation in research, development, and production aspects of biological controls, particularly for propagation of insect pathogens. Thus, we will benefit in a similar manner to other applied phases of entomology: witness the important role of the chemical industry with its contributions to the chemical control of insects. An important contribution to the development of the aggressive rewarding role of the chemical industry in insect control has been the intellectual cooperation of the entomologist and the chemist. A similar liaison between the entomologists and the industrial microbiologists, biochemist, and engineer, is an infrequent association, however, a relationship which is absolutely necessary to cultivate.

The responsibility to establish a flourishing industrial facet of pathogen utility in control programs falls upon your shoulders and mine. What are your contacts, as an entomologist or insect pathologist, with a representative of an industrial or other public or private organisation capable or providing large quantities of pathogens? For those of us in academic areas, how often have we discussed the need and possibilities for use of pathogens with an industrial representative? How many representatives of industry, with any interest in the utility of insect pathogens, have investigated the possible cooperative efforts with a research scientist in a public supported organisation?

Truly, it is the personal elements, interdisciplinary, public and private where integration must be further explored and exploited. It is on the personal level that an intellectual

balance of basic and applied research efforts should be developed. Clearly, the *role* of pathogens in balanced or integrated control programs, beyond limited introductions in attempting to attain a balanced or harmonious state, can depend entirely upon the *role* of those who are capable of providing quantities of effective insect pathogens.

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THE RELATION OF INSECT INFESTATION TO THE GROWTH AND YIELD OF PLANTS AND CROPS

LOSS OF ECONOMIC YIELD IN CROPS

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This paper is substantially the economist's plea for more economic information in scientific papers; particularly those in applied entomology. All too often some vital factor needed by the economist is missing, such as yield, area of plot, number of plants or grading.

The amount of food eaten by an insect population of pest status and the amount of economic damage done by the same population as a pest, bear a relationship to each other, but not necessarily a direct one, and we have selected three examples to illustrate economic points in this field.

In a study of three lepidopterous pests of cabbage (1), the authors' object was to find out the relative amount of damage done to cabbage crops by three pests *Pieris rapae*, (the small white), *Plutella maculipennis* (the diamond back moth) and *Trichoplusia ni* (the cabbage looper). Much more damage was being done by *Plutella* than had been thought previously to be the case.

We have extracted certain figures from this paper and worked them over to give the table below: The Canadian authors established the food intake of the three caterpillars, that on average *Plutella* had five generations to three in both the other species and the number of caterpillars per plot of 49 plants, which we have assumed to be 49 square yards. Our general argument is not affected if our assumption proves to be wrong. We have also assumed a potential crop of 8 tons marketable cabbage for the early crop and 12 tons for the late crop. We then get the following figures:—

Insect	*Food eaten per insect per annum gms*	*Population per acre*	*Food eaten per acre per annum kilos*
Pieris rapae			
Early crop	3·289	24,300	80
Late crop		532,000	1,751
Plutella maculipennis			
Early crop	0·438	16,400	7
Late crop		1,248,400	547
Trichoplusia ni			
Early crop	5·087	400	2
Late crop		36,300	185
Totals:			
Early		41,400	89
Late		1,817,100	2,483

Crop	*Potential weight per acre*	*Actual saleable wt. per acre*	*Damage done*		
			Directly eaten		*Actual*
			wt.	%	%
Early	8	0·8	89kg.	1	90
Late	12	3·0	$2\frac{1}{2}$ tons	21	75

The results show a wide spread, between the *direct* damage done (the amount of leaf eaten) and the economic damage done, (leaves fouled and quality spoiled): in the early crop 1 per cent of leaf eaten destroyed 90 per cent of the crop's value and in the late crop 21 per cent of the leaf eaten destroyed 75% of the value: there are bigger colonies of insects in the late crop.

Some interesting studies of population and food intake of aphids (2, 5) on a field of beans infested with *Aphis fabae* for a period of twelve weeks showed that the average population per stem started at 53, and reached a peak of 7,258; the insects had a life of about 20 days. We have multiplied these figures up and reach some 923 million aphids per acre over the period, each extracting 34 mg of sap. This gives 31 tons per acre, a large sum, most of it water. The economic damage was the distortion of growth, virus disease and the killing of flowers: we cannot put a figure on this, though we have postulated a 15% loss in the table below. The crop and haulm weigh about 3 tons so that the aphids seem to be taking ten times the weight of the crop, but the crop is dry weight and the aphids and sap are largely water.

The sunn pest (*Eurygaster integriceps* Put.) is a serious pest of cereals in the Near East. Vinogradova (3) made some detailed studies of its sap consumption and found that one larva, on the average, consumed 268·9 mgm of sap in the season and damaged 47 grains. She considered 1 larva per square metre capable of causing economic damage, so taking the crop at 1 ton per ha. and the number of grains as 30,000 per kilo, we find that 10,000 larvae per hectare consume 2·7 kilos per hectare of sap and that they damage 470,000 grains per hectare, out of a potential crop of 1 ton consisting of 30 million grains. The damaged grains spoil the sample and are open to infection by fungi and mites. The direct damage (loss of weight) is 0·27%; the indirect damage is $\frac{470{,}000 \times 100}{30 \text{ million}} = 1{\cdot}6\%$. The apparent discrepancy is explained by the relative water content of the sap extracted and of the dry grain harvested.

On these figures it is likely that the weight of sap extracted is about equal to the economic loss, which however is not consistent with the theory that 10,000 insects per hectare cause economic damage, for a loss of 0·27% of a crop could not be noticed; even 1·6% loss can scarcely be measured. Such are the problems that arise when we begin to examine these figures in this way.

Summarising the results we get the following table:—

Crop and Pest	*Per Cent Damage*		*Ratio Direct: Economic*
	Direct	*Economic*	
Cabbage caterpillars			
Early crop	1	90	1:90
Late crop	21	75	1:3·6
Bean Aphid (sap)	1000	say 15	1:0·015
Sunn Pest	0·27	0·16	1:0·6
	or 0·27	0·27	1:1

Another economic factor of importance in this matter of pest control is the smoothing of the production curve, the breaking of a "glut-shortage sequence". Where pest incidence is erratic and over a wide range the amount of pest present can have a big effect on production. We have already drawn attention to this in the case of plums in England (4) and we summarise the argument here. Spring frosts and aphid attack were the problems of plums at the beginning of this century. Means of control were poor: successive gluts and scarcities of plums were common, by no means all due to biennial bearing, and are reflected in the prices.

At first the variation from year to year is low: this was the period when tar oil winter wash made aphid control easy. The variation then rises; perhaps because red spider was becoming a pest as a result of the tar spraying. This in its turn is controlled, and the variation drops. A slight increase in variation from 1951 onwards suggests the present difficulties with pesticides, but the increase is hardly significant. Standard annual production is a very real benefit of the control of pests by any means, which is not generally realised.

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RELATION OF *OSTRINIA NUBILALIS* (HBN.) TO THE GROWTH AND YIELD OF *ZEA MAYS* (L.)

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The relation of the European corn borer to the growth and yield of corn has been studied in some detail in Minnesota during the past 15 years. Several aspects of our results will be discussed here primarily to illustrate the complexity involved. It should be mentioned first, (1) that larval feeding may result in injuries on different parts of the host plant, depending upon the stage of plant growth when feeding takes place, and (2) that the insect has two generations a year. Because of the difference in the time of their occurrence, borers of different generations will feed on different parts of the plants.

Effects on Ear Growth and Stalk Breakage. An observation plot was prepared with two plantings two weeks apart of the same variety of corn (4). The numbers of egg masses deposited on the plants by moths of the two generations were checked. Later, at harvest time, the ear growth and the per cent of stalks broken were recorded. The results show that more egg masses were laid on the early planting than on the later planting during the first generation, and that the reverse was true during the second generation. The ear growth was significantly reduced due to borer feeding. This reduction was much higher in the early planting than in the late planting. But a much greater proportion of plants broke over in the late planting than in the early planting. Therefore, the first generation feeding was more responsible for reduction in ear growth and the second generation for plant breakage.

Stalk breakage near the ground reduces the efficiency of machine picking. It was further found that the direction of breakage in relation to the tractor movement is important. Breakage in the row with the tractor movement, breakage in the row against tractor movement, and breakage across the rows reduced harvest efficiency by about 50%, 25% and 10% respectively.

Tunnelling in the ear shank causes the ear to break over or even break off (3). Many of such ears will not be picked up by the machine. Both stalk breakage and ear dropping will become more extensive as the plants dry in the fall. Therefore, with the same level of borer population, the efficiency of picking decreases as the harvest is delayed.

Effect on Vegetative Growth. Observations were conducted on two varieties each planted on two different dates (6). The height of plants in the different plots was definitely reduced in proportion to the level of borer infestation. To our surprise, the reduction in plant height was initiated before the larvae had even entered the stalk, or before any stalk

tissue had been directly injured. This phenomenon led us to believe that some chemical effects originated by larval feeding on the leaves might have been transmitted throughout the entire plant.

Comparison of the length of different internodes indicates that most of the reduction was in internodes bearing the first ear and in the tassel; in other words, the reduction was in the internodes near the male and the female reproductive organs. These organs demand a large amount of nutrients, and such demands over-rule the need for growth of the vegetative parts. Thus any disturbance in the balance of nutrients supply due to borer infestation would be expected to have a greater effect on the internodes near the reproductive organs than on other internodes.

The chemical nature of the effect of borer injury on plants is further pointed up by another series of observations. A technique was developed to establish borer infestations directly in the stalk (1). Tunnels were first made in the stalk with an electric drill, and an egg mass nearing hatching was introduced into the tunnel. Some larvae survived and started their own boring. With this method, borer infestations were established at known locations in the stalk and at known times. In one study the yield of plants with artificial tunnels only and those with tunnels and borers was compared (2). Results show that the borer-free tunnels cause 1-2% reduction in ear growth, while borer-inoculated tunnels cause more than 10% reduction. The amount of physical destruction by the borer-inoculated tunnels was only about twice as much as by the borer-less tunnels. These results again suggest that borer injury involves more than just physical destruction of tissues. The same study also show the significance of the site of infestation in the insect-host relation. Borers established near the ear showed higher survival and faster development, but those established near the base of the plant caused a greater reduction in ear growth.

Effect on Stalk Rot. A further aspect of the borer-corn relation is the introduction and spread of microorganisms into the plants by tunnelling borers. The fungi *Fusarium graminearum* Schw., and *Diplodia zeae* (Schw.) are known to cause stalk rot which reduces ear growth.

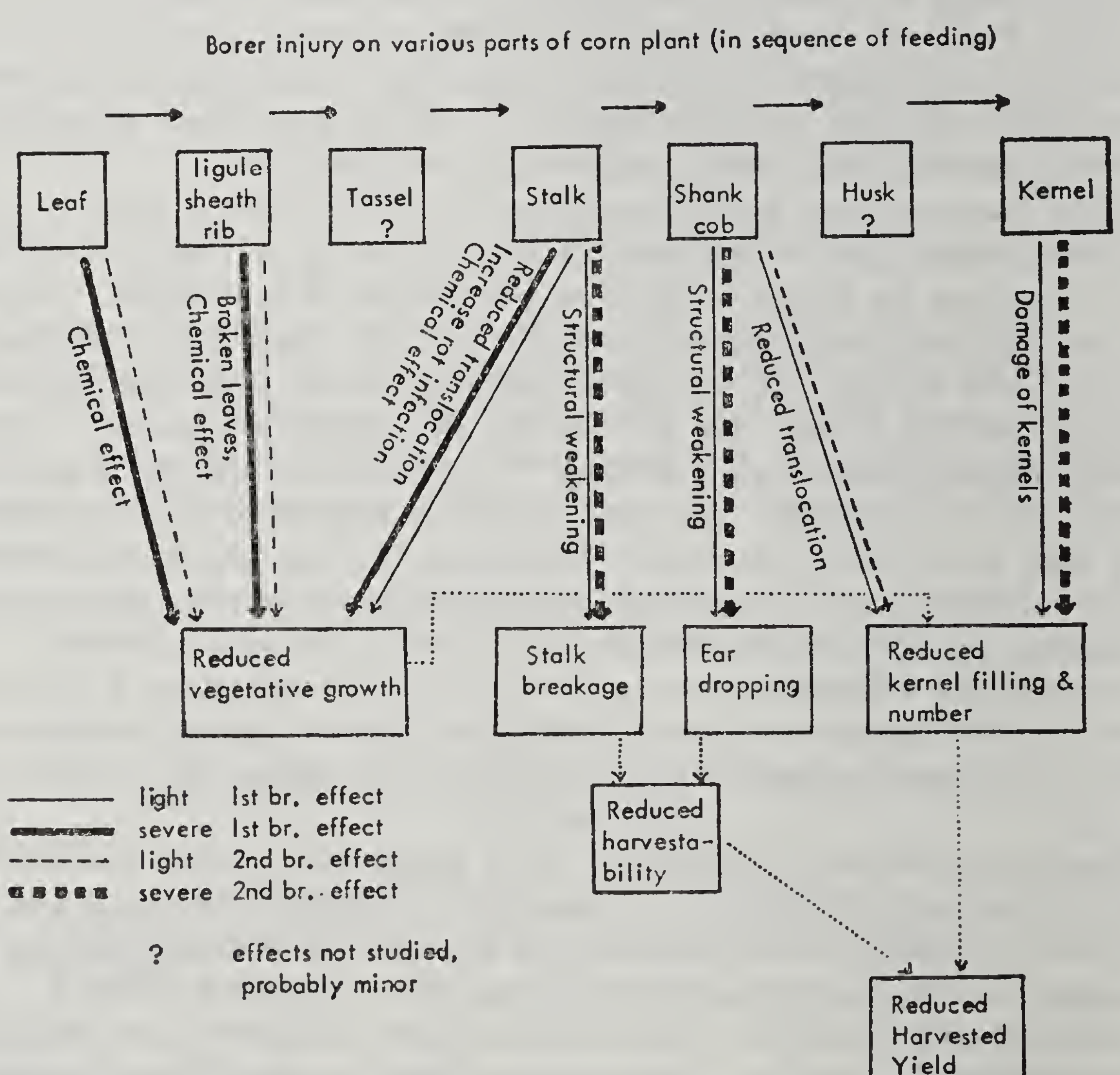

Fig. 1. Effect of borer injury on different parts of corn plant on harvested yield.

The importance of corn borer in initiating and increasing the stalk rot has been demonstrated by early workers. Our new technique described earlier permits us to study the inter-relationships of corn borer, stalk rot and corn in a more precise manner and in greater detail. Much work is still in progress, but one point is already clear, namely, while the borer initiated and increased stalk rot, these micro-organisms also promoted the growth of the borers (7). The implication of this mutualism is that while both the borers and the pathogens individually affect plant growth, the effect of their concurrence is likely to be greater than the sum of their individual effects.

The aspects of the relation of this insect to the growth and yield of corn described so far are summarized in figure 1. They by no means cover all borer-corn relationships. For example, the criteria for evaluating damage on corn for table use (5) or for silage (Chiang and Kolari, unpublished data) will be very different.

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THE RELATION BETWEEN PLANT INJURY IN MAIZE AND OVIPOSITIONAL PREFERENCE OF *OSTRINIA NUBILALIS* (HBN.) (EUROPEAN CORN BORER)

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Experimental studies, conducted in the field, have revealed that infestation of maize by larvae of the European corn borer prevented infestation by a later generation of the corn borer. Data on the phenomenon over a three year period from three states have been summarized (1).

Data on oviposition by moths on plants that had been infested and on plants that had been kept free of infestation by spraying with EPN show that plants which were free of infestation by borers in the first generation had more eggs laid on them than did plants which had been infested by borers of the first generation. Further, the data show that plants during first generation had only a small number of egg masses laid on them by moths of the second generation, and the heavier the infestation the fewer the eggs laid. Thus the reduced infestation due to injury is apparently related to oviposition.

The present paper describes observations and experiments which throw some light on the avoidance of injured plants by ovipositing moths. Patch and Pierce (5) developed a method of obtaining oviposition by corn borer moths held in small cages. An oviposition cage 24 in. × 12 in. × 12 in. was modified to produce an apparatus for testing the reaction of female corn borer moths to odors—an olfactometer. With the use of the olfactometer, the attraction or repellence of an odor was determined by the number and the location of the egg masses laid. Healthy corn plants enclosed in bell jars gave off an odor which attracted female corn borer moths.

In an effort to localize the attractant which was being given off by the uninjured corn plants, juice was expressed from fresh green corn plants by means of a laboratory press capable of exerting a force of 12,000 pounds per square inch. The press was taken to the corn field in a truck and the juice extracted from the corn plant was frozen with the aid of dry ice within three minutes after the plant was cut. Juice from the leaves, from the stalk, from the silk and from the tassel and from the whole plant was tested in the olfactometer. In 128 tests of the juice with the olfactometer no positive reaction was observed and many trials showed a slight

negative reaction. Moreover, juice from borer-infested corn plants and uninfested plants was tested in the olfactometer; no difference could be found in the responses of the moths to the juice extracted from infested and uninfested corn plants.

It has not yet been possible to demonstrate the presence of the attractant in any way except with a living plant and the olfactometer since damage to the plant in any way made it repellent. This prevented the use of plant extracts taken by any of the usual methods. A chamber was therefore constructed to obtain the volatile material from the plant without injuring it. The chamber was a box made of plexiglass which could be placed over a corn plant. Air which had been drawn over activated charcoal was passed through the chamber and then through a dry ice distillery. The chamber was operated at night from 10 p.m. to 3 a.m.

The unusual response of female moths in avoiding injured plants was discovered when corn borer moths were exposed to odor from an injured plant. The moths moved away from the odor of injured corn plants and deposited eggs in a gradient away from the port of entry of the odor. Water of guttation from injured corn plants and a distillate of corn juice from injured corn plants, made in a glass water bath distillery and dry ice trap, were tested in the olfactometer and were also found to repell ovipositing corn borer moths.

Chemical identification of the attractant and the repellent has been attempted. More attention has been given to the repellent. Identification of the repellent was not possible by means of paper chromatography because of difficulty in the resolution of spots. The repellent liquid gave a faint color with ninhydrin, but this was not the ninhydrin positive reaction for amino acids. The sulfanilic acid test for ring structures was faintly positive. A positive reaction was obtained with the ferric chloride test for aldehydes as described by Fiegl (2).

A test of the odorous material given off by undamaged plants gave a negative test with sulfanilic acid and a negative test with ferric chloride.

With a beckman Quartz Spectrophotometer Model DV at wavelengths from 200 millimicrons to 300 millimicrons, there was an absorption band for the repellent liquid at 260 to 280 millimicrons.

For the present we can say only that in the repellent a ring structure is apparently present and that the active substance might be an aldehyde.

We are not ready at this time to make a statement about the attractant.

Large scale dispersal flights of corn borer moths were observed in Southern Minnesota during two consecutive summers. In one instance a flight was measured and covered an area of 24 miles by 11 miles. Apparently these flights originated in areas of Iowa where first generation infestation of corn was very high, nearly 100 per cent infestation. Our laboratory studies have suggested that the repellent odor from these infested injured plants may be the cause of the dispersal; the ovipositing moths were apparently repelled by the odor from the injured plants and were therefore induced to leave the area.

The evidence advanced through the studies on corn borer are in line with the view expressed by Johnson (3). He presented the view that most exodus flights are taken by insects when there is no adversity within a population. He saw migration as an evolved adaptation of adult insects which allows dispersal to areas where there would be reduced intra-specific competition. In 1963 (4) Johnson expressed a similar view in a somewhat different way when he said "migratory flight seems to have evolved as an adaptation designed primarily to relinquish habitats destined to become unsuitable and to secure new ones".

The evidence advanced in this paper offers an explanation for the dispersal flights of corn borer moths which fits the suggested explanation of Johnson.

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FORECASTING FRIT FLY (*OSCINELLA FRIT* L.) DAMAGE: THE RELATIONSHIP BETWEEN EGG NUMBERS AND SHOOT ATTACK

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Although *O. frit* has been the subject of many investigations, surprisingly little attention has been paid to methods of forecasting the damage.

Frit fly lays its eggs on the plants, usually within the coleoptile, and on the soil close to the plant. Could egg numbers be used to forecast the attack? Or better still, since it is much easier to find and to count "plant" than "soil" eggs, could "plant" eggs alone be used for forecasting? These were the two questions which we tried to answer in 1961-63.

Method. A series of small plots sown during early summer were sampled for Frit fly eggs and then screened to prevent further egg laying. The shoot damage was assessed visually about 2 weeks later when the plants were still in the 1-2 shoot stage. In all there were 28 sets of observations. The oats (variety Condor) were dressed with organo-mercury and the soil was a medium loam.

We made use of copper rings (16 mm diameter, 12 mm deep) to obtain egg figures for individual plants and to facilitate the recovery of eggs from the soil. A ring was placed just below soil level round each of 15-20 seedlings chosen at random soon after emergence; several days later, the rings with the plants and soil were lifted for examination. These samples were first examined under a binocular for eggs on the plants ("plant "eggs), and then by flotation in saturated magnesium sulphate for eggs in the soil ("soil" eggs).

Results. Significant correlations were established between the egg numbers and damage. Some of the correlation coefficients and regression formulae are shown below. The egg figures are expressed in square root transformation.

1. Total number of eggs/plant (X): number of damaged shoots/100 plants (Y)
   $r=0{\cdot}72$, (26 DF)
   $Y=(54{\cdot}0\pm9{\cdot}6)\ X-3{\cdot}2\pm5{\cdot}1$
2. Number of "soil" eggs/plant (X): number of "plant" eggs/plant (Y)
   $r=0{\cdot}51$, (26 DF)
   $Y=(0{\cdot}51\pm0{\cdot}17)\ X-0{\cdot}03\pm0{\cdot}61$

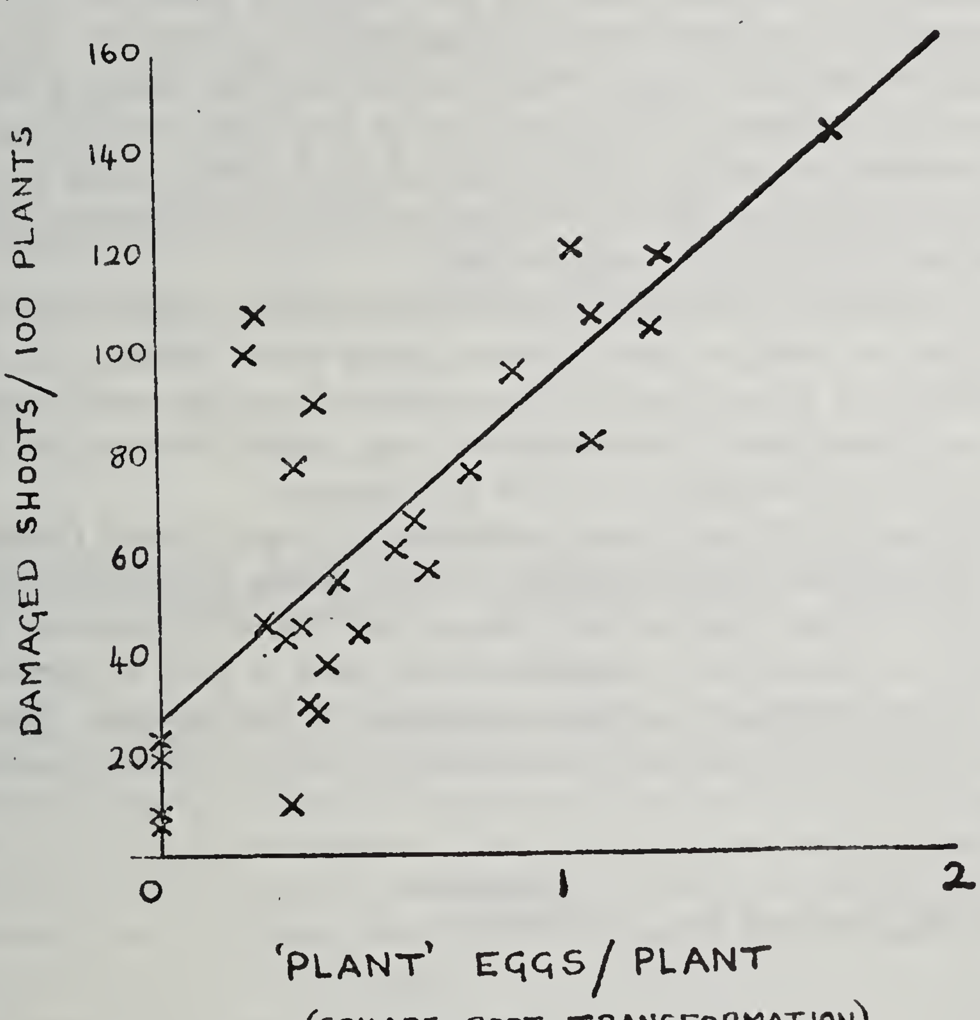

Fig. 1. Frit fly: Regression of "plant" eggs on damaged shoots.

3. Number of "plant" eggs/plant (X): number of damaged shoots/100 plants(Y)
   $r = 0{\cdot}79$, (26 DF)
   $Y = (68{\cdot}7 \pm 10{\cdot}5)\ X + 26{\cdot}0 \pm 4{\cdot}9$ (see Fig. 1)

Conclusions. Although fairly wide confidence limits are attached to the formulae, the results suggest that egg numbers can be used for forecasting Frit fly shoot damage. In view of the practical difficulties of sampling for "soil" eggs, the close correlation between "plant" eggs and damage is of particular interest. However, due to the high ratio (4:1) of "soil" to "plant" eggs, at least in our experiemnts, with the existing formula "plant" eggs could only be used to forecast more severe attacks; even with only one "plant" egg found on 15 plants, 28-58 shoots/100 plants could be expected to be damaged.

THE EFFECT OF LEPIDOPTEROUS STEM BORERS ON THE YIELDS OF CEREALS IN N. NIGERIA

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Guineacorn (*Sorghum vulgare*) and millet (*Pennisetum typhoides*) are the most important cereals grown in N. Nigeria and, north of the rivers Niger and Benue, they provide the staple diet of most of the population. Maize (*Zea mays*) is of less importance in this northern area than it is in the south but production in the north is increasing.

From 1956 to 1959 the effects of lepidopterous stem borers on the yields of these three crops were studied in a series of field trials at Samaru, near Zaria (11·01 N., 7·44 E.). Because of its economic importance, particular attention was given to the assessment of losses in yield of guineacorn which might be attributed to attack by larvae of *Busseola fusca* (Fuller). In 1956 1957 and 1958 experiments showed that, contrary to expectation, bored stems gave significantly higher yields of grain than did stems which had escaped damage by borers. Further investigation of this relationship in 1959 indicated that this failure to associate stem borer attack with loss of yield in guineacorn resulted from a combination of selective oviposition by female *B. fusca*, which tended to lay more eggs on larger stems, and the ability of these stronger plants to tolerate considerable mechanical damage without any drastic reduction in yield. Plants attacked by larvae of the first generation gave significantly lower yields than those which had not been bored but boring by larvae of the second and third generations, which accounted for the majority of the infections, did not reduce yield.

This situation contrasts sharply with that which prevails in maize, where *B. fusca* is known to have a drastic effect on yield in most of Africa south of the Sahara. It also contrasts with the situation in millet in N. Nigeria which, when planted and harvested early, is little affected but, when grown as a late-planted, late-maturing crop, cannot tolerate the high borer populations of *Coniesta ignefusalis* (Hampson) to which it is exposed.

These observations, which have been published in greater detail elsewhere, (1), indicate the need to relate assessments of borer damage to yield before deciding the status of the pest in any particular crop. In the case of indigenous varieties of guineacorn grown within the traditional agricultural system of N. Nigeria, stem borer is not, at present, a major factor limiting yield. The introduction by plant breeders of late-planted, short-term, improved sorghums may well change this pattern and expose the crop to greater damage by stem borers and by other pests.

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THE ASSESSMENT OF THE EFFECT OF INSECTICIDES ON INFESTATIONS OF *HYLEMYA ARAMBOURGI* SEGUY (DIPT.—ANTHOMYIDAE).

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The larva of *Hylemya arambourgi* is a stem-borer of barley in Kenya. Its life-cycle differs principally from that of dipterous stem-borers of the temperate regions in being very short and uninterrupted by diapause, so that a crop is subject to a continuous attack.

Assessments of control measures were made by counting dead shoots per unit length of row and expressing these as a percentage of the total shoots for analysis. This method gave satisfactory comparisons of treatments at any one time, but showed inconsistencies in successive assessments and in predicting yield.

Increases in infestation were proportional to the number of shoots available for attack and the prior presence of dead shoots diluted further attack, causing apparently greater increases in infestations which developed after a degree of insecticidal protection. Since dead shoots could persist for up to a month, their diluting effect, followed by their disappearance, resulted in a modification of the apparent infestation, especially since the later dead shoots would persist after the disappearance of the earlier "diluting" shoots.

The susceptibility of shoots varied. The youngest shoots were comparatively immune since they had been exposed to attack for so short a time, while later in growth, actual resistance developed. Hence, suceptibility to attack increased with time and only later decreased. Due both to a traumatic response and to reduction of intra-specific competition through thinning, attacked plants produced more shoots over a longer period than did unattacked plants, so that for a time, attacked plants had a reduced overall susceptibility to attack.

In unprotected plants, the number of shoots present had no effect on the percentage infestation, but in protected plants the percentage infestation increased with increasing shoot number. This was probably due to a dilution of the insecticide.

The above factors interact and, coupled with the variable persistence of dead shoots and fluctuations in the intensity of attack, cause variations in the apparent infestation, which will be manifested differently in different treatments.

The inconsistencies in assessments indicate that they can carry little predictive value for estimating yield. Also, in Kenya conditions, delayed maturation need not be deleterious and an unprotected crop may eventually produce sufficient ears to give a good crop. The differeence is then reflected in the unprotected crop taking longer to reach maturity, and in uneven ripening. Further, since protected and unprotected crops are passing through similar stages of development at different times, and hence under different weather regimes, the unprotected plants may benefit through reaching critical stages of development during more favourable weather conditions. This could further obscure the effects of shoot losses.

THE EFFECTS OF CABBAGE ROOT-FLY (*ERIOISCHIA BRASSICAE* BOUCHE) ON SUMMER CAULIFLOWERS GROWN ON FERTILE ALLUVIAL SILT SOILS

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Almost half the cauliflowers produced commercially in the United Kingdom are grown on the fertile silt soils of Holland, Lincolnshire. The routine treatment against cabbage root-fly (*Erioischia brassicae* Bouché), in the district, is a dieldrin root dip at planting time.

First generation eggs are laid from about the first week in May onwards; numbers usually rise abruptly to a peak at the end of the month and gradually decline during the first fortnight in June. Crops of summer cauliflowers planted out late in spring may be completely killed by the first generation larvae, especially if the early growing conditions are poor and are followed by warm dry weather and early emergence of root-flies.

The two replicated experiments on the variety Delta, outlined in this paper, are part of a long-term investigation into the effects of damage by root-fly which is less severe than the death of the plants. Relatively slight damage can affect the total weight of cauliflowers harvested, curd size and quality, and the earliness or lateness of cutting.

Seed was sown the previous autumn and half the seedlings were pricked out into beds in the normal way and the rest into prepared soil blocks, for overwintering under cold glass frames. In spring, dieldrin wettable powder root dips (2 oz. of 50% wettable powder in 10 gallons of water), and field drenches of 0·03% dieldrin emulsion were used on the transplants drawn from the plant-bed; frame-drenching before planting out and field drenching were compared on the soil block treatments.

All of the drench treatments gave a good control of root-fly, and an increase in yield over the corresponding controls; the produce was also of a more uniform quality and size. Root-dipping caused a reduction in yield in 1962, when root-fly attacks were late and the plants had been set out in the field early in the season. In 1963, when the root-fly attack was heavier and earlier, root-dipping did not give an adequate control.

In 1962 the soil block treatments outyielded the transplants, but in 1963 when all the plants were allowed to grow larger before cutting, these differences were not so marked. However, in both years the soil block plots yielded a higher proportion of their marketable produce within the first two weeks of cutting, and frame drenching gave slightly earlier yields than did field-drenching. There was evidence in 1963 that severe root-damage caused the curds to be smaller.

No plants were killed by the root-fly damage in either of the experiments. It seems that if the variety Delta is planted out sufficiently early in spring, and if growing conditions immediately afterwards are favourable, cabbage root-fly is unlikely to be a serious commercial hazard on the silt soils of Holland, Lincolnshire. Unfortunately, there are some years when unfavourable conditions for the plants combine with early appearance of the root-flies when damage may be much more severe than was recorded in these experiments.

BETWEEN-SEASON VARIATION IN YIELD IN RELATION TO PEST ATTACK IN THE SUDAN GEZIRA

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Cotton is grown as an annual cash crop in the Sudan Gezira on irrigated land and is of dominant economic importance to the Sudan. In spite of irrigation and a high degree of standardization of agricultural practices there have been tremendous variations in average cotton yield from year to year, within the last twenty-five years the range in yields extending from 1·5 to 6·8 k.p.f.*

Several long term experiments, the Gezira Observation Plots, were laid down in 1939 with a primary objective of determining the major causes of year to year fluctuation in yield. To this end a large number of environmental factors and plant growth parameters were measured each year as well as crop yield.

The economic yield of the cotton plant is the seed-cotton and in particular the lint growing from the seed coat. Variation in economic yield is, however, related closely to variation in plant size. Moreover though the cotton crop, sown in August, is picked during January, February and March most of the between-season variation in total seed cotton yield can be accounted for in terms of variation in total plant growth before the end of December (1).

On basic physiological grounds total plant dry matter production, hence weight, might be expected to depend in large measure on the amount of effective photosynthetic tissue borne by the plant during the season (2). Multiple regression analysis of the relationship between yield and leaf weight at the G.O.P. in the Northern Gezira (Turabi G.O.P.) showed that although the bulk (c. 70%) of the variation in yield over the years 1943/44 to 1960/61 could be accounted for in terms of variation in the weight of healthy leaves per plant in November and December, the relationship did not hold to the same extent if total leaf weights, i.e. including

pest and disease damaged leaves, were used as independent variates. This indicated that leaf damaging pests and diseases were important in determining crop yield. The percentages of leaves obviously damaged by jassid (*Empoasca lybica*), thrips (*Caliothrips* spp.), blackarm (*Xanthomonas malvacearum*) and leaf curl (a virus disease) had been recorded at regular intervals in each year. Multiple regression of yield on these leaf damage data showed that at Turabi 70% of the year to year variation could be accounted for by regression on jassid and thrips damage, and at the Gezira Research Station (Central Gezira) 66% of the yield variation could be so accounted for. This indicates that in the absence of jassid and thrips attack yield variation would have been very substantially less and most of the low yields would have been avoided. To prove this data from pest free plots in all years are needed but are not available. However experiments to test the effect of anti-jassid spraying on yield were carried out in many of the years. In the years in which the heaviest jassid damage symptoms were recorded at Turabi G.O.P. very substantial responses to anti-jassid spraying were recorded (Table 1).

TABLE 1
Jassid damage symptoms at Turabi G.O.P. (4 worst years) and maximum responses obtained by spraying in other experiments

Crop season	*% leaves with damage symptoms at Turabi G.O.P.*		*Yield response to spraying in other experiments*	
	Mid Oct.–end Nov.	*End Dec.*	*K.p.F.*	*% increase over control*
1946/47	11·5	98·4	2·49	100%
1960/61	22·0	97·9	2·97	72%
1947/48	26·7	82·6	2·27	84%
1945/46	10·2	64·5	1·95	43%

The yield figures for 1960/61 refer to the effect of five sprays at the Gezira Research Station (3) since no experiments were carried out nearer to Turabi in that year. The other results are from large scale spraying trials in the Turabi region (Snow and Taylor (4)). These responses to spraying support the view that in years of heavy leaf damage symptoms jassid attack does indeed markedly affect yield. They do not necessarily show what the yield would have been in the absence of jassid attack since even the five insecticide sprays given in 1960/61 did not keep jassid numbers at the low level characteristic of some other years.

At Hag Abdulla G.O.P. in the Southern Gezira most of the yield variation over the years can be accounted for on the basis of variation in plant leafiness but much less of it is explicable in terms of variation in recorded pest and disease damage (1). It seems likely that whitefly attack which, though not recorded in the G.O.P.s, is frequently heavy in this region, may be of importance in this respect.

In studying seasonal variation in yield in relation to environmental factors such as insect attack it is important that all the relevant environmental variables are measured. Lack of data on one factor may mask any relationship between yield and other measured variables even when such relationships actually exist. In many circumstances it is likely that the importance of a particular environmental factor may be affected in some years when some other factor becomes yield-limiting. In this case regression analysis may give misleading results quite distinct from the "spurious regression" that may arise due to association of the measured dependent and independent variables with an unmeasured factor affecting both. Experimental investigation of the relationships under study by observational and regression analysis methods is therefore of great importance.

*1 k.p.f. = 304 lb. per acre

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SOME METHODS OF ASSESSING CROP LOSS CAUSED BY PESTS

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There are several procedures for the assessing of crop loss by pests. That based on comparing yields of two sets of plants, growing simultaneously in the same conditions, one set infested or injured by a pest, the other not, is dealt with in this paper.

Sometimes plants are killed in large compact masses (e.g. by locusts); then the percentage loss in yield equals the percentage of killed plants. To assess such crop losses Znamensky (1926) recommended that the size of the destroyed area be multiplied by the average yield per unit area of the other parts of the fields. Where pests do not kill the entire plant, or where only single plants are killed, the percentage loss in yield does not usually equal the percentage of injured or killed plants. Some examples of yields of attacked and unattacked plants, using different methods of assessment, are quoted below.

1. *Naturally attacked plants compared with unattacked plants.*

A. Direct comparison of the yields of any naturally infested and any naturally uninfested plants. Barber (1911) estimated losses in sugar cane yield caused by *Diatraea saccharalis* Fab. in the U.S.A.

B. Selective oviposition. Where there is selective oviposition, assessment of losses by direct comparison of the yields of any uninfested and any infested plants can be misleading, as shown by Comstock (1889), for losses of yield of wheat caused by *Cephus pygmaeus* in the U.S.A.

Various methods of assessment based on a corresponding matching of the injured and uninjured plants have been applied where oviposition was selective: for example, Znamensky (1926) with shoot attack of *Oscinella frit* on cereals in Russia; Judenko (1938) with infestation of hops and millet (*Panicum miliaceum* L.) with *Ostrinia nubilalis* Hb. in Poland; with *Harmelita tritici* Fitch on wheat in the U.S.A. Chamberlain (1941). Golebiowska *et al.* (1959) applied a similar method to determine the yield loss of wheat caused by *Chlorops pumilionis* Bj. in Poland, although no selective oviposition was observed.

C. Compensation. Young plants lost from any cause can be compensated for to some extent by increased growth and yield of neighbouring plants. To assess the effect of gaps, after the plants have been killed, on the yield of the remaining plants, Lubischev (1935) recommended that yields of the plants growing near the gaps be compared with the yield of those growing at a distance from the gaps.

2. *Plants with artificially induced attack compared with unattacked plants.*

A. Artificial infestation. To assess losses caused by *Zeadiatraea grandiosella* Dyar on the yield of corn, Arbuthnot *et al.* (1958) made a field experiment in the U.S.A., in which plants predestined to be injured were deliberately infested with larvae.

B. Simulation of the mechanical injuries. Experiments to simulate the influence on yield of defoliation caused by pests to sugar beet were done in England by Roebuck (1933) and Jones, Dunning and Humphries (1955).

3. *Naturally attacked plants compared with artificially protected unattacked plants.*

A. Protection by screening. To assess crop losses of wheat caused by *Hylemya coarctata*, Raw and Lofty (1957) made field experiments in England. In one, the uninjured set of plants was obtained by screening plots. Plants to be injured were left unscreened.

B. Protection by mechanical treatment. To estimate the losses in yield of cabbage from *Pieris brassicae* L., Judenko (1938) made an experiment in Poland, in which an uninjured set of plants was obtained by periodically destroying the eggs and newly hatched caterpillars on plots of plants predestined to be uninjured.

C. Protection by chemical treatment. Assessment of yield loss attributed to the shoot and grain attack of oats by *Oscinella frit* were done in England from 1953 to 1957 (Strickland 1958). Sets of plants to be protected from injury were sprayed with insecticides.

D. Protection by a combination of mechanical and chemical treatments. Judenko, Johnson and Taylor (1952) estimated the effect of *Aphis fabae* on the yield of beans in England. Plants were kept uninfested mainly by removing aphids daily, but small colonies of aphids were also killed by spraying them individually with nicotine emulsion.

4. *Plants with artificially induced attack compared with artificially protected, unattacked plants.*

A. Field experiments with caged plants. Loss of yield, quality and viability of rice seed attacked by *Oeballus pugnax* F. in the U.S.A., were investigated by Swanson *et al.* (1962) using field cages to cover the plots. Some plots were artificially infested with this pest, whilst others were left untouched.

B. Field experiments with uncovered plants. Neiswander and Herr (1930) investigated the loss in yield of maize in the U.S.A. from *Ostrinia nubilalis.* To obtain an uninfested set of plants, eggs were removed from some plants; different sized caterpillar populations were obtained on other plants by infesting them with different numbers of eggs.

Conclusions. The best method of assessment depends upon the species of pest, the type of injury and the particular crop, but to find the best method for each, several methods should be compared.

THE EVALUATION OF POTENTIAL LOCUST DAMAGE TO AGRICULTURE

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With the objective of evaluating the potential damage likely to be caused by the Desert Locust (*Schistocerca gregaria*) (as an example, for the sphere of this investigation includes all other locusts and grasshoppers of economic importance) the concept of a Crop Vulnerability Index (C.V.I.) was conceived.

The C.V.I. represents the relative vulnerability of a crop to locust damage between unit geographical areas in an "average" infestation year, the reference geographical area being one bounded by meridians and parallels 1° apart and termed a "degree-square".

The frequency of occurrence of Desert Locust swarms for the 20 year period 1939-58 in each "degree-square" has been calculated for each month of the year and this constitutes the basic locust data.

The distribution of a particular crop is mapped from agricultural statistics in the form of "dot-distribution" maps, each dot representing 10,000 acres (c. 4,000 has.) from which the acreage cultivated within each "degree-square" is calculated.

It can be shown for most of the key areas of potential Desert Locust damage that the number of swarm reports during one month is proportional to the cube of the frequency of past swarm occurrence in any "degree-square". Since damage can be expected to be proportional to the number of swarms reported in any one area, the C.V.I. for any month and "degree square" is arithmetically defined as the product of the cube of the probability of swarm occurrence and the crop acreage, divided by 100 so as to give a working figure of reasonable magnitude. The total C.V.I. is the sum of the monthly values covering the growing period of the crop.

These values have so far been calculated for three major crops, wheat, sorghum and cotton and roughly estimated for others. The estimated C.V.I. value for the whole of the Desert Locust invasion area from this gives an index value of about 100,000. Since about £1 million damage was caused by the Desert Locust in an average year over the 10 year period 1949-58, which represents approximately 100,000 acres of cultivation destroyed, then the C.V.I. value as previously defined can be tentatively translated into potential crop acres destroyed.

From the somewhat sparse knowledge of the relative fluctuation of intensity of infestation, based on the relative number of swarm reports between years in sample areas, a factor of about 10 times the average C.V.I. could be reached over wide areas in peak plague years, as was demonstrated in India and Iran in 1962 when damage exceeded the calculated C.V.I. values by about 10 times. Locally in extremely bad years the C.V.I. can be exceeded by about 100 times due to the combination of the swarm-number factor (10 ×) and the swarm-size factor which also increases ten-fold in certain areas and at certain times.

WHEAT BLOSSOM MIDGES IN IRELAND

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In southern areas, notably in counties Cork, Waterford and Wexford, *Contarinia tritici* (Kirby) occurred in enormous numbers in 1951 and caused such serious damage that the yield in some areas was no greater than the amount of grain sown as seed. *Sitodiplosis mosellana* (Géhin), although common, has not been recorded as abundant enough to cause noticeable loss. In the years following this outbreak, data were obtained from a number of centres in the country which showed a steep decline in population in the years following 1951 and a gradual rise from 1954 onwards to a peak in 1956. This 1956 peak population was economically insignificant in all districts and was actually lower in Cork and Wexford than in some other areas, which was a reversal of the 1951 position. There has been no serious abundance of the pest since 1951.

Barnes has shown that the population of wheat blossom midges in the field of permanent wheat at Rothamsted Experimental Station fluctuated in a cyclic manner, giving peaks of abundance at intervals of about five years. In order to determine if similar population trends occur in Ireland under crop rotation conditions, population data were obtained since 1954 from the same district in Co. Dublin, but not from the same field. The figures for *C. tritici* exhibit a cyclic pattern covering two years of peak populations, 1956 and 1960. The populations of *S. mosellana* fluctuated in a more irregular manner. Barnes obtained a more regular cyclic pattern when he added the data for both species, but the numbers of *S. mosellana* encountered in Ireland were so small that adding the figures for both species would have little effect on the *C. tritici* curve and, therefore, the data for each species are presented separately.

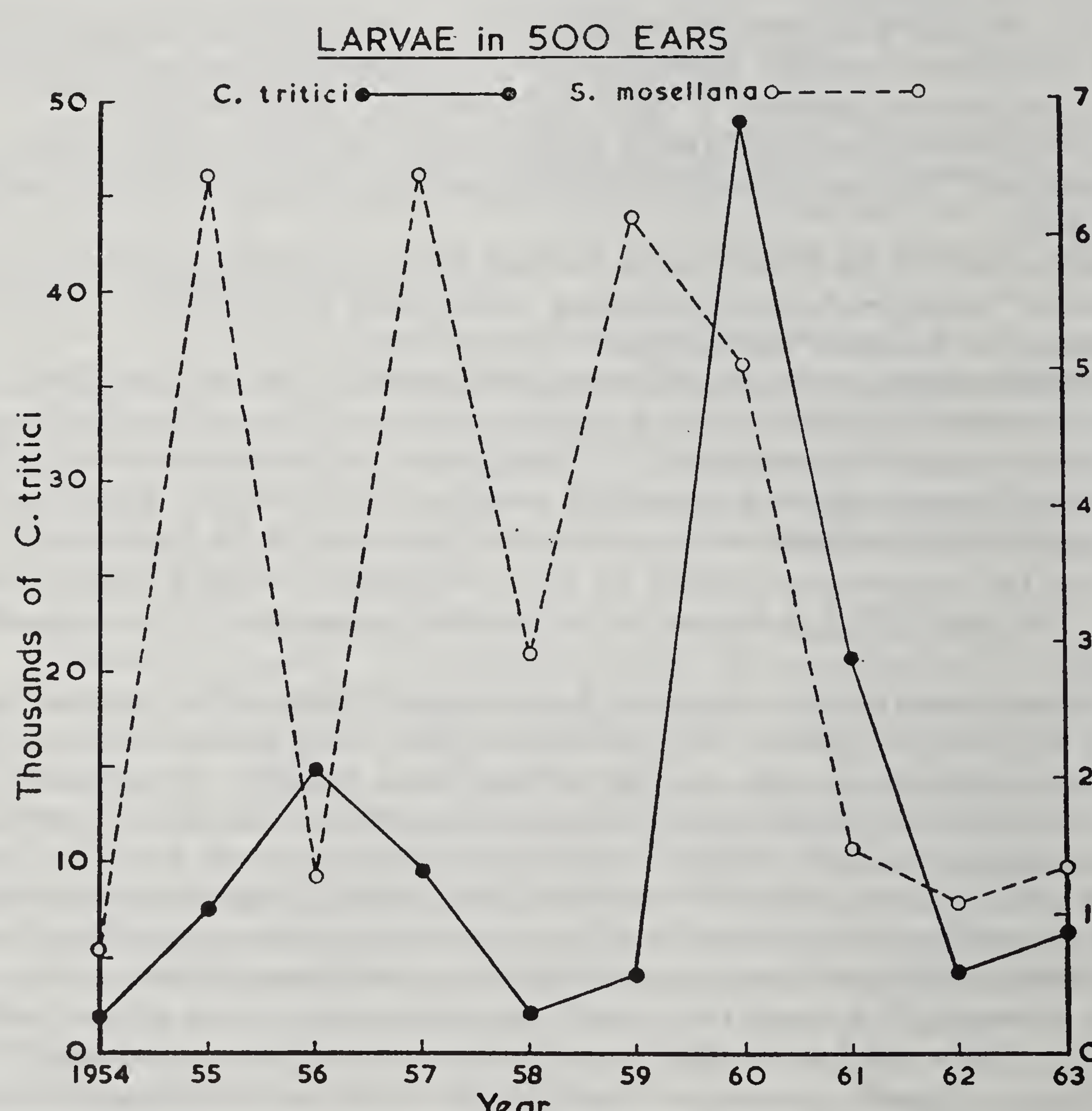

Fig. 1. Fluctuations in populations of wheat blossom midges.

Samples, consisting of 100 ripe ears selected at random from the centre square yard of each plot, were taken from experimental fields where an appreciable amount of infestation was found. These samples were used for the estimation of yield differences between wheat which suffered midge attack and wheat protected from midge attack by spraying. Each experimental field contained 20 unprotected plots and 20 or more protected plots and samples were taken from 7 such fields, not all in the same year. The results obtained did not show significant differences in yields between protected and unprotected plots, although up to an average of 4,500 larvae per 100 ears, corresponding to an estimated 10% of fertile florets infested, were encountered.

Control measures against wheat blossom midges seem to be unnecessary, except on the rare occasions when epidemics occur. In the protected plots referred to above, 88% to 99% reduction in the number of *C. tritici* larvae was achieved by a 0·13% D.D.T. spray applied at the rate of 100 gallons per acre. The spray was applied when the most forward ears commenced to appear through the sides of the leaf sheaths. Good results (92% reduction) were also obtained by a spray applied as early as 1 week before commencement of ear emergence.

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THE EFFECTS OF *METATETRANYCHUS ULMI* (KOCH) ON APPLE TREES (VARIETY COX)

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There is relatively little experimental evidence available in the United Kingdom on the effects of *Metatetranychus ulmi* on apple trees (1). During 1960-63 trials were done to measure the effects of *M. ulmi* on small, pyramid type apple trees (Variety Cox) grown on the regulated hedge system at 12 ft. × 3 ft. spacing. The orchard was on heavy soil overlying chalk with a pH of 8·1.

Method.—Plots of four trees were used with ten replicates in a randomized block layout. Ten plots received the full spray programme for pest and disease control and a further ten plots were covered with screens during the application of sprays likely to affect *M. ulmi* although they received the full sulphur (fungicide) programme. Different plots of trees were used each year. The acaricides used in the orchard were: 1960, malathion (petal fall) and phenkapton (30th June); 1961, dimethoate (petal fall) and malathion (17th July); 1962, malathion (petal fall) dimethoate (4th June) and phenkapton (16th July); 1963, dimethoate (petal fall) and 7th July. In each year the screened trees which had not received these organophosphorus materials were sprayed with gamma BHC at petal fall for apple sawfly and woolly aphis control. No sawfly or codling damage was recorded on the plots. Woolly aphis was a serious problem only in 1963 but there was no significant difference between treatments.

Samples of leaves were examined usually at monthly intervals during May to September, and the number of mites and eggs was estimated using a leaf brushing technique. At harvest the fruit from all plots was weighed, graded and the total number of apples recorded. In 1960 and 1961 an estimate was made of fruit quality. In the late autumn of 1960 and 1962 extension growth measurements were also made.

In 1960 and 1961 heavy infestations of *M. ulmi* gave significant yield reductions ($p = 0{\cdot}05$). In 1962 the yield reduction was not quite significant at the 5% level. In 1963 infestations were very low and no significant effect on yield was recorded. The yield loss was caused by a reduction in the total number of apples produced. Significant correlation coefficients of 0·62 and 0·46 (18 D.F) were obtained for yield and mean infestation per plot in 1960 and 1961

respectively. The results suggest that in the trial orchard where Cox are grown on the regulated hedge system on a soil not ideal for fruit growing, heavy mite infestations had a direct effect on yield.

No obvious differences were recorded in fruit size or quality. In 1960 extension growth measurements showed a significant ($p=0{\cdot}01$) reduction in growth on the unsprayed trees, there was no significant difference in extension growth in 1962.

Results.—A summary of the four years results is given in the table.

TABLE
Summary of Results

Year	*Mites and eggs/leaf*				*Date of Peak Infestation Unsprayed*	*Mean Yield per plot (lb)*			% *loss of yield*	% *reduction in number of fruit*
	Mean		*Peak*							
	Unsprayed	*Sprayed*	*Unsprayed*	*Sprayed*		*Unsprayed*	*Sprayed*	* (±)		
1960	68	13	168	44	23/6	55·8	80·6	4·7	30·7	29·8
1961	87	24	252	58	12/9	20·9	32·1	2·9	34·8	31·9
1962	32	1	63	1	17/7	19·9	23·2	1·1	14·2	13·4
1963	6	1	10	1	12/8	27·6	28·9	2·2	4·5	5·2

(*SE of Treatment means)

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THE EFFECTS OF FOLIAR AND SOIL APPLICATIONS OF DIMETHOATE AND MENAZON ON APHID INFESTATION, VIRUS INFECTION AND THE YIELD AND QUALITY OF TOBACCO

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Field tobacco plants were treated with dimethoate and menazon by spraying the foliage, by mixing the insecticides in the planting water, and by adding them in granular form to the fertilizer. Useful reductions in the amounts of rosette and bushy top infection, and increases in yield and quality, were obtained following three weekly sprays with dimethoate at 6 oz. active ingredient per acre, or with menazon at 8 oz; an application of 64 oz. of menazon to the soil at the time of planting produced similar results. The effects on aphid colonisation of spraying with both dimethoate and menazon declined sharply one week after treatment, though they were measurable for two weeks and there was an advantage in applying the three sprays during the first three weeks after planting, rather than spreading them over six weeks. The effects of the soil applications lasted longer than the sprays though three to four weeks persistence was the most that could be obtained with the formulations that were tested. Planting water treatments gave better aphid control in the period immediately after planting than granules mixed with the fertiliser; the greater persistence hoped for from the granules was not obtained and the results suggest a need for granules with an initial fast and then a later slow rate of release. Improvements in yield and quality were clearly related to the amount of aphid control exercised by the treatments during the early stages of growth of the plants, and the resultant effects on virus infection. Infection is most damaging when it occurs during the first three weeks after planting and the spray treatments were superior to the soil treatments because they were more effective in controlling aphid infestation during this critical period.

STATUS OF THE GRAPE PHYLLOXERA IN NORTHEASTERN UNITED STATES

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The grape phylloxera, *Phylloxera vitifoliae* Fitch, has proved highly injurious to horticultural varieties of grapes derived from *Vitis vinifera* L. in Europe, California and elsewhere when grown on *V. vinifera* roots. The insect is native to eastern North America, where its original hosts included various species of native grapes, of which *Vitis labrusca* L. is typical. Little has been reported on the economic status of phylloxera in grape plantings occurring within the original habitat of *P. vitifoliae.* The absence of any comprehensive paper on the species except one on biology by Riley (1874) is in itself indicative of the fact that it has not been considered a major pest in this area.

The principal commercial variety of grape grown in New York is Concord. It belongs to the so-called Labruscan group (Bailey). The exact origin of this variety is unknown but it is a hybrid and, like other Labruscans, possesses many of the characteristics of *Vitis labrusca,* including an apparent tolerance to the phylloxera. Concord is usually propagated and grown on its own roots.

In common with all crops, the yields of grapes in New York vary widely between vineyards. In surveying the possible causes of these variations, interest has developed recently in determining whether the phylloxera was a possible cause, and if so, to what extent.

Phylloxera was found present on the roots of practically all bearing plantings in the principal grape growing district bordering Lake Erie. Infestation in Concord is limited to the root infesting form that produces galls on the fibrous root. The insect does not infest the leaves of this variety. The majority of vineyards surveyed had populations usually ranging between 2 to 50 nymphs and adults per 25-gram sample of fibrous roots. Sample populations of 150-200 nymphs and adults have also been encountered. In general, the higher populations have been found on the Howard Series of soils which are deep and gravelly in nature, with good to excessive drainage and the rooting depth is 5 feet or more. A fairly close correlation was established between population density and vine vigor, and in turn, to fruit yield. Thus, as vine vigor or yields increase, there is a corresponding increase in phylloxera incidence. From these and additional observations, the writer has reached the tentative conclusion that the phylloxera, usually, is of small economic importance in most Concord plantings in New York.

Observations have been made on the depth distribution of the insect on Concord roots in two soil types. These included one of the preferred gravelly soils and a less preferable soil, Caneadean, which is a quite heavy clay type, somewhat poorly drained and with a "hard pan" layer occurring at a depth of 14 to 30 inches. In the former soil 80% of the phylloxera galls and nodosities were found in the upper 12 inches while 9% occurred in the 12 to 24 inch layer; a few galls were found at a depth of 74 inches. In the clay soil, almost all the root galls were limited to the 12 inches of soil lying above the "hard pan" layer.

SECTION 9b INDUSTRIAL AND STORED PRODUCTS ENTOMOLOGY

The following paper was read but the author did not wish it to be published here:
Pingale, S. V. (India). Maintenance of buffer stocks of cereals under the tropical conditions of India.

BIOLOGY OF STORED PRODUCTS INSECTS

SIMPLE POPULATION MODELS AND THEIR APPLICATION TO THE FORMATION OF COMPLEX MODELS

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Mathematical models are essential in the description of population phenomena, and by analogy with classical physics deterministic models may carry far if the more complex models are built of elementary models which are tested in very simplified experiments.

The only generally accepted elementary model is the compound interest model of unrestricted population growth (N = density; t = time; n = generation no.):

$$dN/dt = rN;\ N_t = N_o e^{rt};\ N_n = N_o\ (1+\lambda)^n \qquad (1)$$

used for estimating the intrinsic rate of natural increase (4) and the damage to be expected from a pest (2).

We have two equally simple models of the effect of density on mortality and fecundity.

If the individuals compete for a requisite (food or oviposition sites) without otherwise interfering with one another the fraction of a population surviving from egg to adult and the number of eggs per female is likely to be proportional to the amount of the requisite per individual as measured by the reciprocal of the density (N):

$$y = a + b/N \qquad (2)$$

If the essential part of competition is mutual interference, it is reasonable to assume that the effect on each individual is proportional to the number of individuals interfering and that, consequently, the surviving fraction and the fecundity is proportional to the density (N):

$$y = a - bN \qquad (3)$$

These models of the effect of density were presented by Andersen (1), who showed that they were verified by extremely simplified experiments, the fit improving with increasing simplification.

For the cases where an increase of small densities results in increasing fecundity Fujita (3) has built a double exponential model, and Watt (6) has made his model still more complicated.

As Watt's model is very inspiring especially because he fits it to an extremely simplified

experiment by Ullyett (5) with *Ephestia*, the model and the experiment is confronted below.

Watt's model rests on Fujita's equation (1) (E = number of eggs laid; ε = intrinsic rate of oviposition; P = frequency of copulation)

$$dE/dt = k\varepsilon NP\ (1 - aE)$$

which is not reasonable for *Ephestia*, as its instantaneous fecundity is not a function of the number of eggs in the medium, but of the number of eggs ripe for laying, which in turn depends on age (ε depends on time).

As to the effect of mating (P) Watt considers the first mating only and bases his equation on Ullyett's experiment, but his moths were all taken *in copula.*

Concerning interference Watt derives his equation from investigations of scale insects which remain eating in the same place, and it is not reasonable to apply this to very mobile moths, which get no food.

Thus, the assumptions underlying Watt's model disagree thoroughly with the conditions of Ullyett's experiment. It should be remembered, however, that the model was not derived with a special view to this experiment, and it may agree well with other situations.

A simpler and more reasonable model of Ullyett's experiment is deduced like this:

1. One element describes the decrease of fecundity during the life of a female. The linear function is arbitrarily chosen as the simplest, but any other function may easily be introduced. If y is the instantaneous rate of egg-laying per 2 days, t is time (unit: 2 days), and a and c are positive constants, we have (fig. 1):

$$y = a - (a/c)\ t \qquad (4)$$

2. A second element expresses that undisturbed moths sit quiet most of the time with reduced metabolism. If they are frequently disturbed their metabolism increases and they move about. Consequently the metabolism and hence the rate of egg production depend on density. This is expressed as an effect on biological time by the equation

$$\tau = te^{k(N-N_0)} \qquad (5)$$

where t is chronological time and τ is biological time defined as the time needed at low density ($\leqslant N_0$) to accomplish a biological process which takes the time t at density N. The exponential function was chosen rather arbitrarily by analogy with the effect of temperature on metabolism, and other functions may easily be substituted.

3. As a third element my elementary equation (3) expresses that, owing to mutual interference, the total number of eggs laid by a female decreases linearly with density. That means that the area (fig. 1) enclosed by the t– and y– axes and the line $y = a - (a/c)t$ decreases linearly with $N - N_0$. Keeping c constant we have

$$a = m - n(N - N_0) \qquad (6)$$

In equations (5) and (6) we assume that densities below N_0 have no effect.

We are now able to build a model of Ullyett's experiment, in which he observed the

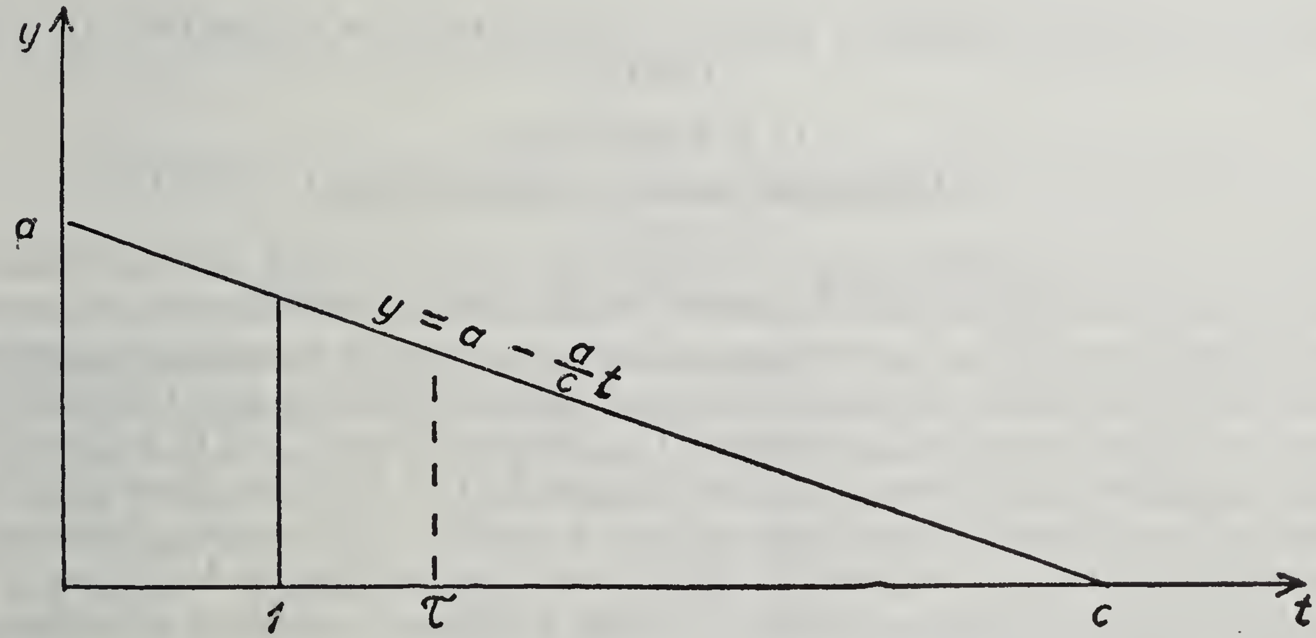

FIG. 1. Instantaneous rate of oviposition as a function of time (age).

number of eggs laid per female during 2 days as a function of the number of *Ephestia kühniella* per test tin.

Taking 2 days as a unit the function (4) (fig. 1) is integrated in the following ways:

$$N \leqslant N_o \qquad A_o = \int_0^1 (a - at/c)dt = a - a/2c; \text{ (no effect of density)}$$

$$\left.\begin{array}{l} N \geqslant N_o \\ \tau = e^{k(N-N_o)} \leqslant c \end{array}\right\} \quad A_1 = \int_0^{e^{k(N-N_o)}} (a - at/c)dt = a\ [e^{k(N-N_o)} - (1/2c)e^{2k(N-N_o)}]$$

$$\tau = e^{k(N-N_o)} \geqslant c \qquad A_2 = \int_0^c (a - at/c)dt = ac/2\ ; \text{ (all eggs laid within 2 days)}$$

Substituting (6) in these formula, we obtain

$$A_o = m - m/2c$$

$$A_1 = (m - n(N - N_o))\ [e^{k(N-N_o)} - (1/2c)e^{\ 2k(N-N_o)}]$$

$$A_2 = (c/2)\ (m - n(N - N_o))$$

which fit Ullyett's results with $m = 101$ eggs, $n = 0{\cdot}926$, $N_o = 18$ moths, $k = 0{\cdot}0692$, and $c = 3{\cdot}24$ (unit 2 days).

Generally this model expresses the hypothesis that when the fecundity increases with density it is due to a larger fraction of the total (decreasing) output of eggs being laid during a short period of observation.

The kind of problems encountered in applying elementary models to field conditions may be illustrated by the following, hitherto overlooked complication: Testing elementary models with experimental populations, the cages should be so small that aggregation is insignificant. However, field populations are aggregated exhibiting a series of densities with probabilities distributed approximately negative binomially. Ordinarily it will be necessary to apply the elementary model to all possible densities and sum up the results weighted with their probabilities calculated from the parameters m and k estimated from samples. In the rare cases when a mean may be used, it is never the ordinary mean (mean per sample, $m = \Sigma x/n$), but the mean density at which the animals live ($\Sigma x^2/\Sigma\, x = m/k + m + 1$).

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THE *CRYPTOLESTES* (GANGL.) (COL.: CUCUJIDAE) OCCURRING IN STORED FOOD

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The six species of *Cryptolestes* found regularly in stored food fall into two main groups. Group A (*C. ferrugineus* (Steph.) and *C. capensis* (Waltl)), whose males have short antennae and laterally expanded mandibles, can develop successfully at relative humidities well below 50%. The males of Group B have long antennae and simple mandibles and the species do not develop at humidities below 50%. Group B/I (*C. turcicus* (Grouv.) and *C. pusillus* (Schön.)) produce a tough silken pupation cocoon whereas group B/II (*C. pusilloides* (Steel and Howe) and *C. ugandae* Steel and Howe) do not construct such a cocoon. The species within each group and sub-group tend not to occur together and if more than one species does occur in any one micro-habitat, the two or three are likely to belong to different groups or sub-groups. Four species have not occurred together.

THE EFFECT OF TEMPERATURE AND HUMIDITY ON THE RATE OF INCREASE, R_M, OF THE RUSTY GRAIN BEETLE, *CRYPTOLESTES FERRUGINEUS* (STEPHENS) (COLEOPTERA: CUCUJIDAE)

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Cryptolestes ferrugineus (Stephens) is the most serious insect pest of stored cereal grains in the Prairie Provinces of Canada.

The rate of increase, r_m, of a strain of *Cryptolestes ferrugineus* from Manitoba, Canada was calculated from data obtained in the laboratory on its oviposition, developmental time, mortality in its developmental stages and sex ratio. Experiments on the effects of temperature were done from the range 17·5 to 42·5°C., inclusive, at 2·5°C. intervals, at 70% r. h.; experiments on the effects of humidity were done at 40 and 90% r. h., at 25, 30, and 35°C. The rates of self-multiplication were obtained using the natural antilog of r_m.

It was calculated that the rates of self-multiplication at various combinations of temperature and relative humidity were as follows: 50 or more times a month at 35°C., 70 and 90% r. h. 20 or more times per month at 32·5°C., 70% r. h. and 30°C., 90% r. h.; 10 or more times per month at 30 and 37·5°C., 70% r. h.; 5 or more times a month at 25°C., 70 and 90% r. h., 27·5 and 40°C., 70% r. h. and 30 and 35°C., 40% r. h.; 3 times per month at 22·5°C., 70% r. h. and 25°C., 40% r. h. There was no increase above the replacement rate at 20°C., 70% r. h.

As the temperature increased from 20 to 40°C., there was an exponential decrease in the developmental time from 14·6 to 2·9 weeks. Developmental time was reduced by 25 to 35% as humidity increased from 40 to 70%, and by a further 5% as the humidity increased from 70 to 90% r.h. No larvae completed development at 17·5°C.; at 42·5°C., only 2 larvae out of 40 completed development, and one of these adults died the day it emerged.

At 70% r. h., the oviposition rate for the first five weeks was highest at 35°C. (nearly 40 eggs per week), 30% less at 30°C., 70% less at 25°C. and 40°C., and 98% less at 20°C. The oviposition rate increased as humidity increased to 90% at 30 and 35°C., in general, but at 25°C. there was no difference in oviposition rates among humidities. The oviposition rate at 30°C., 70% r. h., did not differ greatly from that at 30°C., 40% r. h.

Mortality during development at 70% r. h. was 6 to 12% at 25 to 35°C., inclusive (lowest at 27·5°C.) but increased to 60% at 20 and 40°C.; at 40% r. h. mortality increased from 15% at 25 and 30°C. to 20% at 35°C.; at 90% r. h., mortality was 12% at 25°C., 17% at 30°C. and 5% at 35°C. Profuse mold growth at 90% r. h. undoubtedly affected mortality, particularly at the lowest temperature.

Sex ratio at all combinations of temperature and humidity was unity.

It was concluded that the greatest effects of temperature and humidity on the value of r_m were caused mainly by their effects on developmental time. The effects on oviposition and mortality respectively were next in order of importance.

STUDIES ON THE BIOLOGY OF *SITOPHILUS* SPECIES

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After the discovery (17) that there are two varieties of rice weevil, Takahashi (21) made a series of intensive comparative studies and asserted that each was a distinct species. Further studies were carried out mainly by the workers at Kyoto University with regard to temperature, (23, 25) water content of grain, (2, 14) heat tolerance (9, 24) and sex ratio (3). Recently, the focus of studies was much extended by using many lines of both species obtained from abroad and Japan. *Sitophilus zea-mais* is distributed all over Japan and has two or three generations a year (5, 15, 29). Winter is passed by the adult outside the warehouse (5, 13, 21). After hibernation, some return to the warehouse, but in the south others visit flowers to feed

on nectar (28, 30) and infest standing crops (4, 5, 26). *S. oryzae* is rarely found in the north, but is much prevalent in the south (4, 8, 13, 21) where it normally has two generations a year in the unheated grain. It passes the winter in the larval stage (13, 21) and occurs only indoors partly due to the lack of flying ability. (4, 7, 8). Thus, the heating of rice during the winter is largely induced by *S. oryzae*, and grain temperature often reaches as high as 35°C with a maximum density of 630 adults/100 g of rice (21), as compared with 32°C and 40 adults/100g in *S. zea-mais* (21). *S. zea-mais* develops faster than *S. oryzae* on rice (11, 13, 16, 19, 21, 25) and maize, and more slowly on wheat when species obtained from the same country are compared (1, 11, 12). In addition, *S. zea-mais* gives a greater number of progeny than *S. oryzae* on maize, but fewer on wheat and rice (12).

Of the physio-ecological variations observed among the geographical strains of both species, the variations which were associated with the reduction of body size drew our first interest. The variation in the mean body size among the strains of the same species was much greater in *S. oryzae* than in *S. zea-mais*. However, *S. oryzae* was always smaller than *S. zea-mais* when both were obtained from the same country (10, 11). In *S. oryzae*, male/female ratio of body size is less than unity and the value decreases with the reduction of body size, but vice versa in *S. zea-mais* (12). Furthermore, it seems that the male develops faster than the female in *S. oryzae*, but slower in *S. zea-mais* (12, 16). The inter-specific cross between Japanese species is sterile (22, 27), but most of the inter-crosses among 8 strains of *S. oryzae* and 7 of *S. zea-mais* produced F_1 which showed intermediate characters and required a longer developmental period than the parents. In a few cases, F_2 were obtained. There was a tendency for the reproductive isolation between the species to become stronger as the difference in size became larger (12). The flying ability of *S. oryzae* was generally poorer than that of *S. zea-mais*. Furthermore, Japanese and Formosan strains of *S. oryzae* lacked the ability to fly. The reductions of flying ability and the ratio of hind wing/elytron were correlated with the reduction of body size (6). Though the reproductive rate decreased with the increase of parent density in both species, in *S. oryzae* the effect of density became small with the reduction of body size, but vice versa in *S. zea-mais* (19, 20). Consequently, it may be concluded that the differentiations in *S. oryzae* being associated with the reduction of body size may represent a process of adaptation towards the life in stored products, and that the smallest, such as the Japanese strain, may represent a specific type of this adaptative process.

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THE STEROL REQUIREMENTS OF SEVERAL SPECIES OF *DERMESTES* (COL. DERMESTIDAE)

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Sterols are essential constituents of the cells of most living organisms. The higher animals can synthesise most of the sterols they require but, so far as is known, sterol synthesis does not occur in insects. Consequently, insects require a sterol in the diet although, in some cases, it may be supplied by internal symbionts. In most insects the dietary requirements for sterols can be satisfied by both phytosterols and by zoosterols but in *Dermestes maculatus* Deg. only cholesterol or certain of its derivatives will support complete development. This result, and the fact that cholesterol has been shown to facilitate growth in *Attagenus megatoma* Fab (=*piceus* Oliv.) has led to the generalisation that zoosterols, especially cholesterol, are essential for satisfactory development of all the Dermestidae which normally feed as scavengers of dried animal materials; in fact, larvae of *D. maculatus* have been used for the biological assay of cholesterol. Clayton (1) reviews the role of sterols in insect dietetics.

Some experiments to test the ability of various Dermestidae to develop upon vegetable diets have recently been carried out and the results with six species of *Dermestes:—maculatus* Deg.: *frischi* Kug.; *haemorrhoidalis* Kust.; *peruvianus* Cast.; *ater* Deg. and *lardarius* L.—are now available. Previous investigators have usually worked with groups of insects and have recorded performance in terms of time to pupation or death. I have preferred to use isolated larvae and to record the degree of development achieved. The food comprised 1·5 g. of wheat germ per larva, maintained at 25°C and 65% R.H. The diet was thus rich in sterols but did not, so far as was known, contain any significant amount of cholesterol—as was confirmed by the inability of *D. maculatus* to develop on it.

The results may be summarised as follows:—

D. maculatus and *D. frischi*. Larvae of both species died after a few weeks while less than $\frac{1}{4}$ grown.

D. haemorrhoidalis. Most larvae died when $\frac{1}{2}$ grown, but about 20% became full-grown, pupated and produced deformed adults.

D. peruvianus. All larvae grew rapidly and pupated normally but the adults produced were always deformed.

D. ater. All larvae grew rapidly but most died when fully grown; however, about 20% pupated and the adults produced were apparently normal.

D. lardarius. Normal adults were reared, giving rise to normal eggs and larvae but many adults of the second generation were deformed.

From these results it is clear that much remains to be learned about the sterol requirements of the Dermestidae and the sweeping generalisations that have been widely accepted on the basis of extensive work on a single species are obviously untenable. Further, it is possible to rear *D. maculatus* (producing deformed adults) on cholesterol-free soya flour, indicating (in confirmation of recent American work) the possible importance of campesterol (a phytosterol) in the diet of this insect. However, difficulties encountered in the preparation of chemically pure sterols and recent reports of the identification of traces of cholesterol in plant tissues suggest that results in this field, at the present time, can be accepted only with reservations.

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SOME ASPECTS OF THE BIOLOGY OF *PARALIPSA* (*APHOMIA*) *GULARIS* (ZELL.) (LEPIDOPTERA) IN RELATION TO ITS DISTRIBUTION

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Paralipsa gularis is a pest of various stored products in Asia, Europe and North America. The damage and contamination of foodstuff by its larvae can be very extensive and result in a considerable loss, particularly when such valuable commodities as almonds are attacked. Development from egg to mature larva on groundnuts at 70% R.H. occurs between 15° and 33°C with an optimum near 31°C. Larvae from stock originally collected in a London warehouse, bred in isolation at 22°C and below, went into a state of diapause on reaching maturity. Of those reared above 22°C the proportion going into diapause varied between 29 and 100% according to which of a number of females provided the eggs. Increased larval density during development has been shown to increase the incidence of this behaviour. Larvae in a state of diapause are resistant to low temperatures, 10% surviving three months exposure to −3°C. Completion of diapause occurs most rapidly amongst larvae exposed to 15°-18°C with little if any occurring above 25°C. While most diapausing larvae reared at 31°C had pupated after 3-4 months exposure at 15°-18°C only 25% had done so after fourteen months at 25°C.

This type of facultative diapause behaviour brought on by relatively low developmental temperatures and crowded conditions is well suited to a storage species developing in conditions that may be expected in temperate and subtropical regions. There it may be able to complete more than one generation during the summer, survive low winter temperatures, with completion of diapause ensuring a synchronised emergence in the spring. Considering only this aspect of its biology it may be predicted to occur between the low temperature limit for morphological development and the high temperature limit for the completion of diapause. In the absence of a useful number of records of warehouse temperatures and humidities these limits can be roughly plotted on the basis of ordinary meteorological data if the average of daily maxima and minima of temperature and humidity is taken as the mean temperature and humidity for each month. If areas with a mean relative humidity of 50% or less for 3 months are discounted as being probably too dry for its development it is apparent that the species occurs throughout much of the predicted areas in Asia, Europe and Western North America though it has yet to be recorded in those areas in the Eastern U.S.A. and the southern hemisphere where conditions may be considered suitable. Most of the occurrences beyond the low temperature limit represent infestations in partially heated food-manufacturing premises. The only significant occurrence beyond the high temperature limit for completion of diapause is that in southern India where it does not occur as a storage pest but feeds on Tamarind pods as they ripen on the tree. The occurrence of diapause behaviour amongst larvae from that source is particularly interesting and suggests that the species is closely adapted to the local conditions on the Tamarind trees. This could be the natural habitat. However under the relatively constant conditions that occur in stored food the ability of some larvae to go into a state of diapause is undoubtedly an important factor influencing the distribution and potentialities of *Paralipsa gularis* as a pest.

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PREVENTION AND CONTROL OF INFESTATION IN STORED GRAIN

SOME ASPECTS OF GRAIN INFESTATION IN EUROPE

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The grain infestation problems of Europe fall rather sharply into two divisions:

1. Control of indigenous infestation in farm stores and collecting points in countries living almost wholly on home produced grain.
2. Control of imported grain insects, either by treatment and inspection at the ports of entry or by prophylactic treatment at suitable points in producer countries overseas.

Some examples taken from the United Nations Economic Commission for Europe contrast the positions in various European countries. Yugoslavia with a home production mainly in small farm units of over 3 million tons of wheat and 4 million tons of maize, finds it necessary in some years to import three quarters of a million tons or less, all from U.S.A. and relatively free from insects. In Germany, home production of 4 million tons of wheat, nearly 3 million tons of barley and 2 million tons of oats is matched by total cereal imports of around 6½ million tons, much of which comes from traditional exporters in the middle East, Australia and the Argentine, where infestation problems are more difficult to deal with than in Canada or the U.S.A. Great Britain, Belgium and the Netherlands are in much the same position, as is Germany vis a vis importations of grain.

In Yugoslavia, storage is mostly in wooden room or roof stores on farms and in small concrete silos or brick warehouses. Fumigation with Phostoxin is popular in central stores, aided by clean up sprays of DDT or Lindane, but no protective applications direct to grain are carried out. In France, Lindane is probably the most widely used grain insecticide in the form of smoke generators, sprays and as admixed dusts at 5 ppm. As an example of a large importing country, Great Britain probably has the longest tradition of the struggle against imported infestation, aggravated by conditions induced during two world wars. Close collaboration with overseas suppliers has led to an active system of inspection and prevention of infestation, both by advocating prophylactic treatments at point of origin with pyrethrins and Malathion, and by provision of fumigation facilities at the ports. The situation in Germany is much the same, but the system of compulsory inspection followed by diversion to fumigation chambers of any grain shipments showing infestation above a threshold of 2 insects per kilo is preferred to the making of efforts to persuade the exporting countries to apply protective methods. The German Food Law of 1958 is invoked to support this practice, and the U.S. tolerance level for, say, Malathion at 8 ppm. is not yet officially accepted by the German authorities.

In recent attempts to harmonise international practice regarding residue tolerances for pesticides in foodstuffs, the concept of the Maximum Acceptable Daily Intake (MADI) has been introduced, in which a published minimum effect level on a test animal may be extrapolated by a series of multiplicative factors, to give a figure from which a tolerance can be calculated. This may bear little relation either to the effective field dose required to kill the insect, or to the results of practical toxicological feeding studies no a wide variety of animals which any reputable commercial insecticide necessarily undergoes in the course of the developmental years. The present period of popular clamour and even of political expediency does not provide a favourable climate for jettisoning the well tried system exemplified by the F.D.A. in the United States, suitably modified to meet the more modest resources of European countries. In particular, these remarks apply to the protective treatment of grain.

PREVENTING INFESTATION OF FARM STORED GRAIN WITHOUT USING CHEMICALS

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Between 9 and 11 million tons of grain are produced annually in Great Britain. The tonnage grown per farm is up to 3,500 with an average of 70. Half of the grain is stored until December, 20% remains in March, and there is little carry over from harvest to harvest.

Sitophilus granarius (L.), *Cryptolestes ferrugineus* (Steph.) and *Oryzaephilus surinamensis* (L.) are the most serious insect pests on farms. These are not field pests and although they over-winter they need temperatures of 20°-25°C for rapid development.

During the main storage period, August to March, the mean daily maximum air temperature in a grain growing area (Cambridge) (1) only reaches 21·7° in August. It is 19·4°C in September and lies between 6·7°C and 14·4°C in the remaining months. Some other source of heat is therefore necessary in late autumn and winter for infestations to become established in grain.

Residues are a source of breeding during warm spells before harvest. Temperatures of between 20°C and just over 22°C were found for at least half a day for several weeks between May and July 1963 within a typical farm store.

Grain may be harvested up to 30% moisture content and must be artificially dried for storage. Temperatures up to 40°C were found immediately after drying and the grain normally cools down slowly during storage. Small isolated bins (of about 50 tons) reached 20°C by early November. Blocks of bins took some weeks longer. Large bulks of 500 tons only cooled at the edges if the grain was over 8 feet deep. Damp patches may result from uneven drying and fungal heating may start if grain moisture is about 17%. Recent papers (2, 4) suggested that the heating initiated by fungi is a main agent in producing suitable conditions for the development of grain insects.

Gradients of temperature and moisture content are set up within heating bulks, due to convection currents and conduction. Insects may take advantage of these gradients e.g. Surtees (5) notes that *Oryzaephilus* will congregate in warm or wet grain. Armstrong and Howe (2) calculate that, in initially hot grain which is cooling slowly, 500 *Oryzaephilus* could multiply sufficiently to prevent cooling and initiate heating. When cooling is more rapid, 5,000 *Oryzaephilus* would be needed. Populations of this order have been found in heavily infested bulks and in residues on farms.

Current work suggests that combine-harvested grain contains few grains without mechanical damage likely to make insect attack possible. Grain dust alone is likely to be a satisfactory food for insect pests.

Good design and hygiene in farm buildings will keep residual infestations at a minimum level. If mechanical damage due to combine-harvesting can be reduced, and grain dust is removed, onset of infestations by insects will be retarded.

Grain dried at high temperatures should be cooled to at least 17°C and preferably to 12°C by proper use of the drying machinery or by ventilation from floor ducts when in store (3).

Grain up to 21% moisture content can also be dried on floors, using ducting, at temperatures only slightly above ambient; such grains should also be cooled when drying is complete.

During drying the main aim should be to keep moisture content even and low otherwise heating, due to fungi, may arise and be exploited by grain insects.

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INVESTIGATION OF THE EFFICIENCY OF SPEAR SAMPLING OF BULK GRAIN

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When we first began comprehensive studies of the distribution of insects in stored bulk grain over 20 years ago we first examined heavily infested bulks. Now it has become evident that in order to prevent heavy infestation we must find very small pockets of warm or damp grain, dust and very small numbers of insects. The sampling spears (2) originally used for our early work were based on the standard spear used by the grain trade. Because they had to be pushed up to 6 or more metres into grain, they were of small diameter and had to be inserted four times to yield a 100g sample. Later Burges (1) designed a suction spear which needs to be put in place once only. This spear has the additional advantages of penetrating close to walls and floors, and there is no risk of the sample being contaminated whilst the spear is being withdrawn.

Now that it is apparent that very small numbers of insects may, in a favourable environment, initiate grain heating, it is necessary to try to detect both favourable conditions and the insects. Favourable temperature conditions can be found by inserting thermocouples or thermistors and leaving them in place. Grain sampling, especially for insects, is more difficult. How big a sample is needed? Where does the sample come from and what is the effect of sampling?

To investigate these points a glass fronted box about a metre deep was made and wheat was dyed a number of distinctive colours and placed in the box in layers about 10 cm thick. This grain was sampled at various depths using the two spears mentioned. With the standard spear, the first sample (about 750 grains) from the third layers at 25 cm deep yielded 99% of the correct colour and from the ninth layer at 85 cm, 91% were from the correct layer.

Subsequent samples, however, contained very few grains of the correct colour, but were predominantly from the layer above or even from the one above that. Four samples, taken from 25 cm yielded 28% from the third layer, 54% from the second and 18% from the top. Three samples from the ninth layer yielded 30% from the ninth, 55% from the eighth and nearly 15% from the sixth and seventh and also some grains from the top five layers. The pattern visible through the glass showed that inserting the spear caused a slight depression of the layers and that sampling led to a vertical funnelling rather than to lateral displacement. Evidently with this spear a large number of single samples is preferable to repeated sampling at the "same" spot.

Samples of 300-400g were taken with the suction spear and again the grain was replaced from above so that the sample came predominantly from at least one layer above the sampling point. Thus at 25 cm, 53% came from the second layer and 43% from the third, at the bottom (100 cm) 29% came from the tenth layer and 59% from the ninth, 11% from the eighth and the remaining 1% from all the others. Taking a very large sample in small bursts showed the funnelling convincingly. If this spear was pushed in too far and drawn up, it brought up some grain from the lower layers. If the rods were not completely removed and replaced for deeper sampling, about 10g of grain had to be removed at the new sampling point to clear the tube. The results suggest that for samples of over 100g, the opening of the spear should be 10 cm below the point of interest. Since laboratory work indicates that one insect to 100,000g is likely to be dangerous in favourable conditions, 500g samples are probably necessary but these will cause subsidence and certainly prevent sequential sampling over a series of visits at intervals of time.

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INSECT INFESTATION OF STORED RICE IN JAPAN

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Recent production of rice in Japan amounts to about 13 million tons of husked rice. The loss of stored rice by insect attack is estimated at about 5% (4). In the post-war period, Japan imported a large bulk of rice due to her poor production of domestic rice. The amount of imported rice reached a maximum in 1954 of as much as 1·5 million tons. It is considered that some new insect pests had invaded Japan in the post-war period before the inspection of imported stored products was introduced in 1950 under the Plant Protection Law. Since 1955, rice has been fumigated at the ports of exporting countries before or after loading. This treatment of rice lowered the level of insect infestation from 84% for 1951-4 to 27% for 1955-1962, whereas the percentages in weight of infested wheat, barley and maize during 1955-62 were 79%, 85% and 92% respectively.

The insect fauna of imported rice.

The insect fauna of imported rice is somewhat different according to the country of origin. *Alphitobius diaperinus*, *Lophocateres pusillus* and *Corcyra cephalonica* are rather characteristic of the rice from Southeast Asia (8). *Sitophilus granarius* is found only on the rice from the U.S.A. and the Mediterranean countries. *Tribolium castaneum*, *Sitophilus zea-mais*, *Tenebroides mauritanicus*, *Oryzaephilus surinamensis* and *Cadra cautella*, are all common on imported rice irrespective of the countries of origin. The frequencies of *S. oryzae* relative to those of *S. zea-mais* were 5/1, 2/2, 4/12, 32/374 and 1/27 on barley, wheat, rice, maize and oil seeds, respectively.

Furthermore, *S. oryzae* and *S. granarius*, but not *S. zea-mais*, are found on Australian barley and wheat. Half of the barley and rice shipped from U.S.A. was infested with *S. oryzae*, but most of the maize was infested with *S. zea-mais*.

Insect infestation of stored rice and the status of the important pests.

In Japan, rice is usually stored husked in straw bags piled one upon another in tiers. The water content of Japanese rice is relatively high, 14·6-16·5%, as compared with that of imported rice which ranges from 12-13%. In summer, the grain temperature rises up to 28-9°C in the south; 23-4°C in the north (10). Therefore, the damage caused by insects to stored rice is of the greatest concern in central Japan and southwards. Investigations made in Kinki district in central Japan showed that *S. zea-mais* was the commonest on rice, wheat and barley. The frequencies of *Oryzaephilus surinamensis*, *Tribolium castaneum* and *Plodia interpunctella* were significantly high on rice as compared with those on wheat and barley. Furthermore, the former two and *Cadra cautella* were more frequent on polished rice than on husked rice, but *P. interpunctella* was found equally on both types of rice (6).

S. zea-mais and *S. oryzae* are the most serious pests of stored rice. The former is distributed all over Japan, but the latter is found rarely in the farm storages in central Japan and northward; but it is common under conditions in flour mills (9). The range of distribution of *Rhizopertha dominica* is limited to the warmer part of Japan than that of *S. oryzae*, though this borer can be found in half of the mills in Kinki district (9). The damage caused by this borer was considerably reduced after the war, but even in the pre-war period, it occurred only in the commercial warehouses in urban areas in the southern part of Japan (10, 13). As regards the moths which are injurious to the stored grains, they may be named in the following order of decreasing importance, *P. interpunctella*, *C. cautella*, *Aphomia gularis* and *Sitotroga cerealella*. Kiritani *et al.* (9) have shown that the mills dealing with imported cereals harbour many insect pests that are foreign to the domestic fauna. None of the following can be found in domestic storages: *Alphitobius diaperinus*, *A. ovata*, *Laetheticus oryzae*, *Palorus subdepressus*, *Tribolium confusum* and *Anagasta kühniella*. In addition, the fact that most of the mills were first established after the war due to the necessity of treating a large bulk of imported wheat and barley suggests that these have been introduced and became established during recent years on the imported grain. Other tropical species that are considered to be recently established in Japan are *Lophocateres pusillus* (14), *Araecerus fasciculatus* (5, 14), *Alphitophagus bifasciatus* (7), and *Carpophilus hemipterus* (3). Kiritani (6) reported that individuals of *T. castaneum* which were collected on imported rice were significantly small as compared with those on domestic rice. The measurement of populations bred under comparable conditions has shown that

Japanese *T. castaneum* is significantly larger than the foreign ones (Table 1). A preliminary cross experiment between the Japanese and the small strain was successful and produced progeny. The presence of an endemic type of *T. castaneum* is very interesting when we consider that *T. castaneum* is the commonest species on various kinds of products arriving in Japan and that it would have a good chance of invasion. *Sitophilus granarius* was first recorded in 1923 on imported rice from U.S.A. (12). Immediately after this, the existence of this weevil in flour mills dealing with imported wheat was reported from several places in Japan (2). However, there is no evidence of establishment of *S. granarius* at present (7). There is no reliable record of the occurrence of *Corcyra cephalonica* in Japan. *Trogoderma granarium* has been reported once on stored rice by Nakayama (11) and recently it was discovered in three breweries. It is certain, however, that both can be excluded from the natural Japanese fauna.

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Table 1

Geographical variations of *Tribolium castaneum* in the width and length of prothorax and the ratio of width/length with reference to *T. confusum*.
Measurements were made on 100 insects bred on whole wheat flour at 30°C for several generations.

Species	*Origin of country*	*Commodity*	*Width mean ± s.d.*	*Length mean ± s.d.*	*Ratio of width/length*
T. confusum	Japan	wheat flour	22·81 ± 1·18*	16·59 ± 0·94	1·37
	S. Africa	wheat bran	22·47 ± 1·23*	16·39 ± 0·57	1·37
T. castaneum	Japan	rice bran	23·79 ± 1·08	16·47 ± 0·72	1·44
	Nigeria	peanut	21·48 ± 0·96*	15·73 ± 0·67*	1·37
	Thailand	sesame	21·03 ± 1·00*	15·24 ± 0·75*	1·38

*significant at a 99 per cent level from Japanese *T. castaneum*.

THE INFLUENCE OF HUSK DEFECTS ON THE INFESTIBILITY OF STORED PADDY BY *RHYZOPERTHA DOMINICA* (FAB.) (COL. BOSTRICHIDAE) AND *SITOPHILUS ORYZAE* (L.) (COL., CURCULIONIDAE)

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Studies of the biology of *Sitophilus oryzae* and *Rhyzopertha dominica* on varieties of rice grown in the West Indies and British Guiana (1, 2) have confirmed the suggestion of Corbett and Pagden (3) that neither of these pests is able to feed and breed on mature paddy grains with an intact husk, no matter how high the moisture content. Paddy grains with a split husk may be infested by *Sitophilus oryzae* but to a much lesser extent than milled rice. The contrary is however true for *Rhyzopertha dominica* and a paddy grain is much more easily infested, once the

husk has been split, than a milled and polished rice grain. *Rhyzopertha dominica* is therefore usually the dominant pest in stored paddy but is relatively unimportant in stored rice.

Husk defects which render paddy liable to attack by *Sitophilus oryzae* or *Rhyzopertha dominica* may be natural or induced. Natural defects may result from certain growing conditions or may be peculiar to certain varieties and these defects include a failure of the lemma and palea to close properly after blooming or a separation of these husk components on one side of the grain only. Induced husk defects may be caused by insect attack during the growing period or by fungous diseases, but usually they are caused during the harvesting, threshing or drying processes. Thus the varietal susceptibility of paddy to infestation by storage pests may differ according to the way in which harvesting or threshing has been carried out. A variety with a hard husk and, in consequence, a high potential resistance to infestation, may, if the husk is brittle, become infestible to a varying degree as a result of mechanical threshing. Combine-harvested paddy usually contains a higher proportion of grains with split husks, and grains which have been hulled and broken, than does paddy which has been threshed by bullock treading. Although immature or "green" grains, and those with the lemma and palea separated on one side only are liable to infestation by *Rhyzopertha dominica*, the infestibility of a given sample of paddy by this species is related in the main to the proportion of grains with split husks. Experiments in which pairs of *Rhyzopertha dominica* adults were placed on 100-grain samples of paddy having the "average" composition of combine-harvested paddy showed that breeding was confined almost entirely to grains with split husks and that the rate of multiplication was very much lower than it would be in undamaged wheat. These results suggest that it should be possible to relate the proportion of paddy lost in storage as a result of insect infestation to the proportion of grains with split husks present. Such evidence as may be obtained from the literature shows that even though high populations of *Rhyzopertha dominica* adults may develop in paddy, the proportion of grains damaged does not exceed the proportion of grains with split husks which might be expected. When 20 small paddy samples with known proportions of split and other possibly infestible grains were kept continuously infested with *Rhyzopertha dominica* for two years, the number of attacked grains present at the end of this period showed good correlation with the proportion of split-husk grains originally present.

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ON THE INFESTATION OF RICE AND RICE PRODUCTS IMPORTED INTO BRITAIN

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Between 1953 and 1963, 2,508 cargoes of rice from thirty-three countries were inspected for insect infestation during discharge in British ports. Rice from tropical countries, especially Thailand (17% of total cargoes) and Burma (8%) was generally more heavily infested than that from temperate and sub-tropical countries such as Australia (18%), Italy (17%), U.S.A. (13%), Argentina (6%) and Uruguay (4%).

Four species, *Tribolium castaneum, Oryzaephilus surinamensis, Sitophilus oryzae* and *Cadra cautella* (Table 1), occurred regularly on rice from all sources. *Corcyra cephalonica, Tenebroides mauritanicus* and *Alphitobius diaperinus* occurred on rice from the tropics, being replaced by *Sitophilus granarius* and *Plodia interpunctella* on temperate rice. *Trogoderma granarium* occurred frequently on Burmese rice but not on Thai; the reverse was the case for *Ahasverus advena. Paralipsa* (*Aphomia*) *gularis* was found only on rice from Italy and then mainly in 1958. Italian rice was entirely free from infestation in 1962 and 1963. Infestation in rice from the U.S.A. showed a marked seasonal incidence being negligible during winter and spring but rising to

45% during the summer. The relatively high incidence of *Lasioderma serricorne* on U.S.A. rice was probably due to cross-infestation from rice bran and oilcake in Gulf Ports.

During the same period 1793 cargoes of rice bran from twenty-five countries were seen, principally from India (27%), Burma (25%), U.S.A. (23%), British Guiana (5%) and

TABLE 1
Occurrence of insects on rice from principal sources

	Thailand	*Burma*	*Australia*	*Italy*	*U.S.A.*
Cargoes inspected	406	203	429	405	327
Per cent infested	94	100	17	13	17
Number of species	55	40	19	12	20
Occurrence per 10 cargoes inspected					
Tribolium castaneum (Herbst)	7·9	9·7	0·3	0·4	0·6
Oryzaephilus surinamensis (L.)	6·4	4·0	0·3	0·2	0·2
*Sitophilus oryzae** (L.)	4·0	4·0	0·2	(1)	0·1
Corcyra cephalonica (Staint.)	3·4	5·0	(1)	0	0
Cadra cautella (Walk.)	3·1	4·3	0·9	0·3	1·3
Tenebroides mauritanicus (L.)	2·8	5·0	0	(3)	(1)
Alphitobius diaperinus (Panz.)	1·6	3·5	0	0	0
Ahasverus advena (Waltl.)	0·9(38)	(4)	0	0	(2)
Trogoderma granarium Everts.	(3)	2·7(50)	0	0	0
Lasioderma serricorne (F.)	0·6	1·0	(2)	0	0·3
Sitophilus granarius (L.)	0	0	0·2	0·2	0
Plodia interpunctella (Hübn.)	0	0	0·1	0·1	0·1
Paralipsa (*Aphomia*) *gularis* (Zell.)	0	0	0	0·2	0

NOTES:
*Includes records of *S. zea-mais* (Mots.).
Figures in brackets are actual occurrences.

TABLE 2
RICE BRAN
Occurrences of insects per 10 cargoes inspected

	India	*Burma*	*U.S.A.*
Cargoes inspected	480	456	409
Per cent infested	97	99·9	63
Total species	45	48	41
Tribolium castaneum	*9·6*	9·9	*4·9*
Cadra cautella	*5·6*	*5·8*	*4·7*
Corcyra cephalonica	1·8	*5·1*	0·1
Alphitobius diaperinus	1·1	*5·5*	0·1
Lasioderma serricorne	1·0	1·3	1·1
Oryzaephilus mercator (Fauv.)	0·4	1·7	0·2
Tenebroides mauritanicus	0·4	1·4	0·1
Necrobia rufipes (Deg.)	0·3	1·0	(1)
Trogoderma granarium	0·3	1·1	0
Latheticus oryzae Waterh.	0·3	*5·4*	(1)
Plodia interpunctella	(2)	0	0·9

Figures in brackets are actual occurrences.

Egypt (4%). Cargoes from the United States were the least infested, but even so they showed a marked seasonal incidence, similar to U.S.A. rice, over 80% of all parcels arriving during the summer being infested. *T. castaneum* and *C. cautella* occurred most frequently on rice bran from all sources; *Corcyra cephalonica, A. diaperinus* and *Latheticus oryzae* were particularly common on Burmese rice bran (Table 2).

A comparison of the infestation of rice and rice bran from all sources shows interesting similarities and differences related to the food requirements of the various species concerned. *T. castaneum* (rice 7·2; rice bran 9·4 occurrences per 10 infested cargoes), *C. cautella* (4·1/6·2), *Corcyra cephalonica* (2·6/2·6) occurred at about the same rates, respectively, on rice and rice bran; *O. surinamensis* (4·8/0·3), *S. oryzae* (3·4/0·2), *Tenebroides mauritanicus* (2·3/0·8), *Cryptolestes pusillus* (Schoen.) (0·4/neg.) and *Ahasverus advena* (0·5/neg.) were much more common on rice whilst *Latheticus oryzae* (0·2/1·8) was more common on rice bran.

The effects of climate can be minimised and differences due to the foods themselves demonstrated by comparing infestations on rice and rice bran exported from the same countries. For example, in cargoes from U.S.A., Burma and British Guiana, *S. oryzae, O. surinamensis* and *O. mercator* were more common on rice than rice bran, but *O. surinamensis* was relatively less frequent on rice bran than *O. mercator*, due apparently to the latter's greater ability to breed in food of high oil content. The greater frequency of *S. oryzae* on rice is due to its need for whole grains in which to breed.

RECENT EXPERIENCE IN THE USE OF MALATHION TO PROTECT STORED GRAIN AGAINST INSECT ATTACK

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Malathion in the form of a dust has been mixed successfully with grain to protect it from the most common insects pests in Britain. Recently it has been used as an emulsion and sprayed on to grain as it passed on a conveyor belt to a storage floor. In Trial A, the grain had to travel at least 200 yards between the point of application of the spray and the point of storage by way of 4 conveyor belts, 2 bucket elevators and a long chute, but, in Trial B, it travelled only 50 yards by 2 belts and 1 elevator. In both cases the spray was applied at the rate of 9 p.p.m. but much was lost in transit and only 3·3 p.p.m. was present on the storage floor in the first test and 5·5 p.p.m. in the second. It is, therefore, important to spray as near as possible to the point of storage.

Chemical Tests. Samples were taken periodically from the grain during storage to determine the rate at which the malathion broke down. In Trial A, 3·3 p.p.m. was reduced to 1·7 p.p.m. within 5 weeks but remained at this level up to 14 weeks, despite the fact that the moisture content of the grain was 16%. In Trial B, the initial dose of 5·5 p.p.m. broke down to 2·3 p.p.m. in 15 weeks and 1·2 p.p.m. in 22 weeks at 15% moisture.

The insecticide decomposed more slowly than in earlier experiments with malathion dust.

Biological Tests. The addition of batches of *Oryzaephilus surinamensis* to samples of the treated grain confirmed that the grain was effectively protected against attack by this insect for 14 weeks but, in Trial B, mortality began to fall off slightly at 22 weeks, although chemical tests indicated that there was sufficient malathion present to kill this species.

Sitophilus granarius was killed by lower concentrations of malathion than had seemed necessary from previous experiments and mortality of 100% was recorded even at 0·4-2·5 p.p.m. This was maintained for 5 weeks after spraying of the grain but later, the number of deaths fell even at equivalent concentrations. This effect was more marked than with *O. surinamensis.*

O. surinamensis always died rapidly if affected by the insecticide but *S. granarius* only did so for 2 weeks after spraying. After that, 2-4 days might elapse before it was killed by similar amounts of insecticide. During the delay, the insects laid viable eggs which subsequently gave rise to a further generation of adults.

It had been shown earlier that larvae of *S. granarius* can survive the admixture of malathion with grain and continue their development. In a trial with emulsion, larvae of this species and of *Cryptolestes ferrugineus*, which also live inside grains, caused a severe hot spot to develop soon after treatment and the total breakdown of malathion in the damp and heating area.

INFESTATION IN STORED TROPICAL CROPS

THE PRINCIPLES AND PRACTICE OF TROPICAL COCOA STORAGE[1]

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Araecerus fasciculatus (Deg.) and *Cadra cautella* (Walk.) are known to have been present in Ghana at least since 1900, only seven years after the original introduction of cocoa (1). It was not until the 1950's that *Lasioderma serricorne* Fab. first became troublesome, when storage periods were increasing because of the larger crops (2).

The climate of cocoa growing countries is generally favourable for the development of storage insects and moulds in the prepared cocoa. Preparation of cocoa involves killing of the seeds during the fermentation process. During drying moulds develop readily on the outside of the beans but become dormant when drying is completed at about 6% moisture content. If cocoa beans are stored at high relative humidities the moisture content may increase rapidly and at over 8% moulds may develop and cause tainting. At the higher moisture contents insects also breed more rapidly.

In the prevention of infestation in cocoa good hygiene in stores is essential. Fortunately insects develop slowly on cocoa beans compared with indigenous foods, in which the life cycle of the common pests takes only about half as long. Infestation therefore takes longer to become established in stored cocoa. By keeping cocoa stores clear of infested residues and away from local food stores the onset of infestation can be delayed if not altogether prevented.

Maintenance of high temperatures and low relative humidities unfavourable for development of insects and moulds in cocoa stores may be achieved by using dark coloured buildings with controlled ventilation and damp proof floors. All of these three factors, in addition to rendering the shed atmosphere less suitable for fungal development may contribute towards insect control: dark colouring may render internal surfaces too hot for insect harbourages; controlled ventilation, opened during sunny days and closed before sunset reduces increase of relative humidity at night; it also provides sealed conditions desirable for insecticidal fogging or misting; dry conditions at floor level restrict the development of insects in small quantities of debris. Moisture uptake of cocoa beans may also be prevented by enclosing dry cocoa under p.v.c. sheets, ·005″ thick.

Biological studies of *Cadra cautella* showed that emergence of adult moths takes place in the late afternoon and is followed by a dusk flight and mating. Mated females lay viable eggs by the following morning (4).

Pyrethin-piperonyl/butoxide films were ineffective because they only lasted a few hours (3), successful control was obtained by the application every evening of a dry fog derived from 0·5% pyrethrins in odourless white oil, produced by portable thermal fog generators operated from outside the cocoa warehouses. One pint of insecticide is used per 40,000 cubic feet of overall warehouse space. No synergistic effect was found on moths when piperonyl butoxide was included in the formulation (5, 7, 9, 10).

Although this technique controls flying moths it is relatively ineffective against the larvae and against other insects living inside the beans, such as *Lasioderma* and *Araecerus*. Fumigation has therefore proved necessary, particularly to meet the requirements of the principal cocoa importing countries.

A technique of fumigation by methyl bromide has been developed by which it is possible to fumigate safely and effectively 400 ton stacks of cocoa stored in transit sheds in which normal traffic takes place. Stacks being treated are covered with p.v.c. sheets, sealed to the floor with sand snakes. Gas is introduced at a rate of 16 oz. methyl bromide per 1,000 cu. ft. for six hours in stacks not more than 12 ft. high or for twenty-four hours in taller stacks. Circulation of gas by small fans placed in spaces within the stack is necessary for stacks over 20 ft. high. On completion of treatment gas is exhausted by a special mobile gas extraction

unit which exhausts the gas from the stack through flexible ducting. Gas can be removed in thirty minutes from a 400 ton stack (6, 8).

It is important to regulate the period of treatment and dosage of gas not only to achieve a concentration time product adequate for the required percentage kill of the common cocoa pests but also to ensure that inorganic bromide residues remaining in the cocoa beans do not exceed maximum permissible levels laid down by the importing countries.

The methods of prevention and control used in Ghana have been developed in co-operation with the principal users of cocoa beans in order to ensure that the methods of storage and infestation control are such as not to injure the flavour or quality of the cocoa beans.

1. Based on work by J. Rawnsley

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INFESTATION OF SORGHUM IN NORTHERN NIGERIAN GRANARIES

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Most of Northern Nigeria's sorghum crop is stored unthreshed in farmers' granaries constructed of dried earth or various plant materials including grass matting, cereal stems or wickerwork.

One species of moth and 11 of beetles have been found in sorghum heads before storage. These are *Sitotroga cerealella* (Oliv.), *Sitophilus oryzae* (L.), *Rhizopertha dominica* (F.), *Cryptolestes ugandae* S. and H., *Tribolium castaneum* (Hbst.), *Brachypeplus* sp. and *Planolestes cornutus* (Grouv.) (the latter two are doubtful storage pests) which have all been found in the standing crop; *Lasioderma serricorne* (F.), *Typhaea stercorea* (L.), *Oryzaephilus mercator* Fauv., *Palorus* spp., *Tribolium confusum* Duv. Many species of parasitic Hymenoptera have also been found. These insects probably originate from adjoining granaries. Prestorage infestation alone can result in heavy damage subsequently.

Cross-infestation between stores has been demonstrated with *R. dominica*, *C. ugandae*, *S. oryzae*, *T. castaneum* and *T. confusum.*

Large populations of *Sitotroga cerealella* are nearly always found in stored unthreshed sorghum. *Sitophilus oryzae* is another main primary pest. *S. zea-mais* Motsch. is apparently common only in the south. Other important pests include *R. dominica*, which is particularly numerous in the north, *L. serricorne*, *C. ugandae*, *O. mercator*, *T. castaneum* and *T. confusum. Attagenus gloriosae* (F.), *Ahasverus advena* (Waltl.) and *Palorus* spp. (particularly *P. subdepressus* (Woll.)) are occasionally important.

Damage in mud granaries can be reduced by store hygiene which removes residual infestation and by sealing to prevent cross-infestation. However heavy damage will eventually result from prestorage infestation.

Limited success in control was achieved by threshing and by attempts at air-tight storage in local granaries. Sorghum varieties vary in their susceptibility but complete resistance is highly improbable.

Trials were laid down in many farm centres spread throughout the Region and at Samaru to investigate the relative effectiveness of 5, 10, and 15 parts per million (p.p.m.) lindane applied as a "sandwich" treatment using 0·5 per cent kaolin-based dust. The application

rate of 10 p.p.m. was found to give the most effective protection in heads stored for nine months. Less damage usually occurs during the first six months of storage than during the subsequent three months and thus the treatment was sometimes barely economic in grain stored for less than six months. The results of the two main series of Provincial trials are represented graphically in the Figure.

The treatment does not affect viability, seedling growth, or taste and it provides control for storage periods up to 24 months. It is less effective in grass matting granaries than in mud stores.

Malathion at application rates of up to 15 p.p.m. was less effective than 10 p.p.m. lindane. Carbaryl at rates of up to 15 p.p.m. failed to give control. Fumigation using aluminium phosphide tablets resulted in slight control in open mud granaries.

The work culminated in a recommendation being made to the Ministry of Agriculture that farmers should use 10 p.p.m. lindane. This was approved by the Ministry of Health after contamination studies showed less than 2·5 p.p.m. occurs in food prepared from treated grain.

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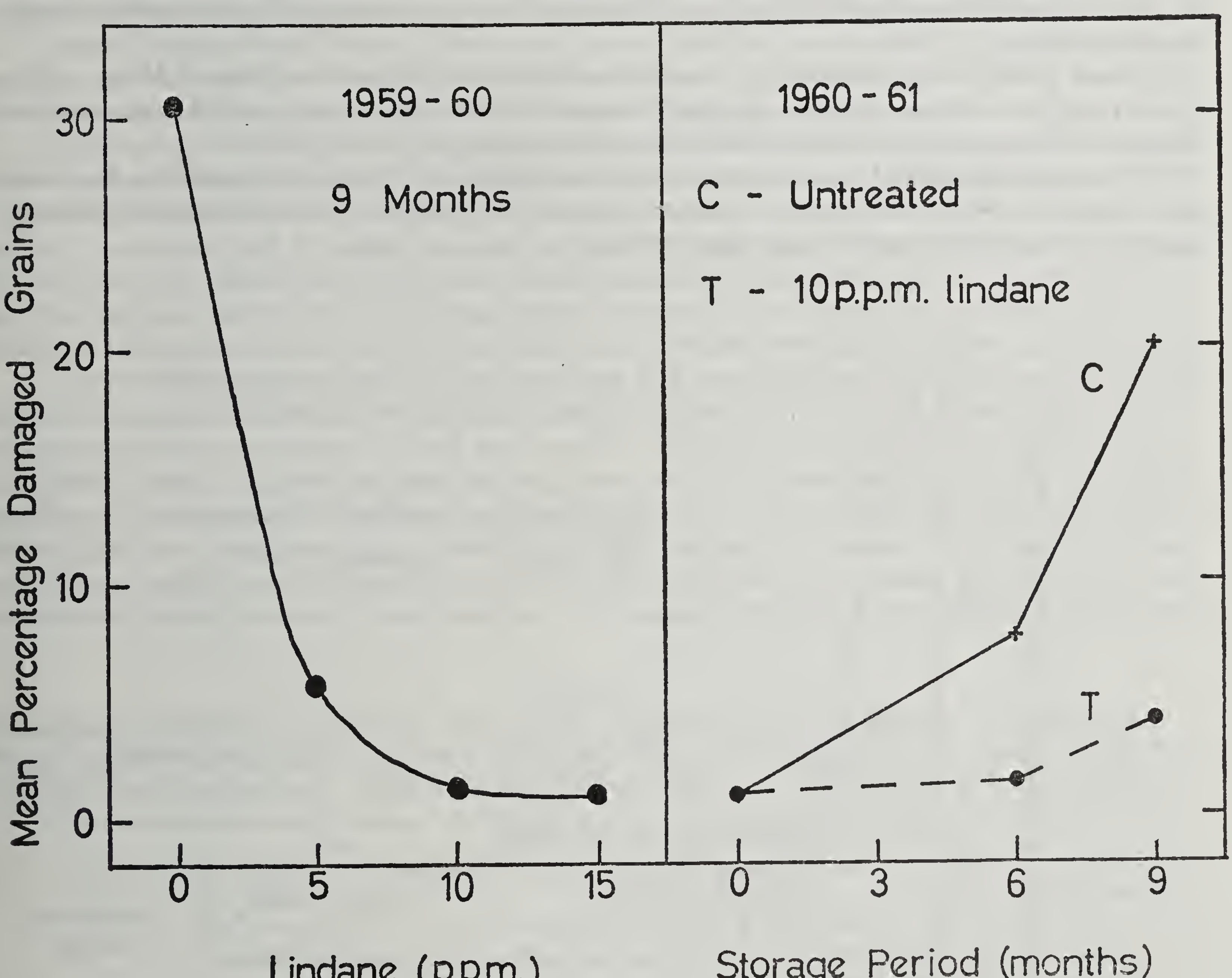

Fig. 1. Effect of lindane "sandwich" treatment on insect damage in unthreshed sorghum stored in mud granaries during two series of Provincial trials.

THE SUSCEPTIBILITY OF GRAIN SORGHUMS TO ATTACK BY THE WEEVIL *SITOPHILUS ORYZAE*

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Grain sorghums, *Sorghum vulgare* grown in the drier parts of the tropics are susceptible to weevil attack. In Tanganyika some varieties appeared to be more susceptible than others (1) because of the physical characteristics of their endosperm.

There are two types of endosperm, mealy and vitreous. Some varieties are mostly hard or vitreous (e.g. Wiru) and the others are almost completely mealy (e.g. UR 477).

The amount eaten by individual male weevils was estimated by weighing at regular intervals. More of the soft grain was destroyed per day than the hard vitreous variety (Fig. 1).

Egg plug counts and X-rays were found to be unreliable methods for counting eggs and young larvae; the conclusion was that a count of the emerging adults was an adequate method of comparing damage by weevils to different varieties of sorghum.

The susceptibility of five varieties to developing larvae was compared at 28°C and 45 per cent R.H. by counting emerging adults. Seed of uniform size in equilibrium with the same relative humidity was used. Groups of fifteen females and five male weevils, at a density of one female per 64 seeds, were placed on samples of seed for four days and then transferred for three days to experimental samples. The procedure was repeated for five varieties replicated four times.

More adults emerged from the mealy than from the vitreous varieties. Many of the parents died on vitreous varieties, possibly because of the slightly lower equilibrium moisture content. At ten per cent moisture content small changes are critical (2).

A recently completed experiment showed that when weevils were cultured in a hard and soft variety of sorghum at the same moisture content (10·5 per cent) there were twice as many emerging adults in the soft as in the hard variety.

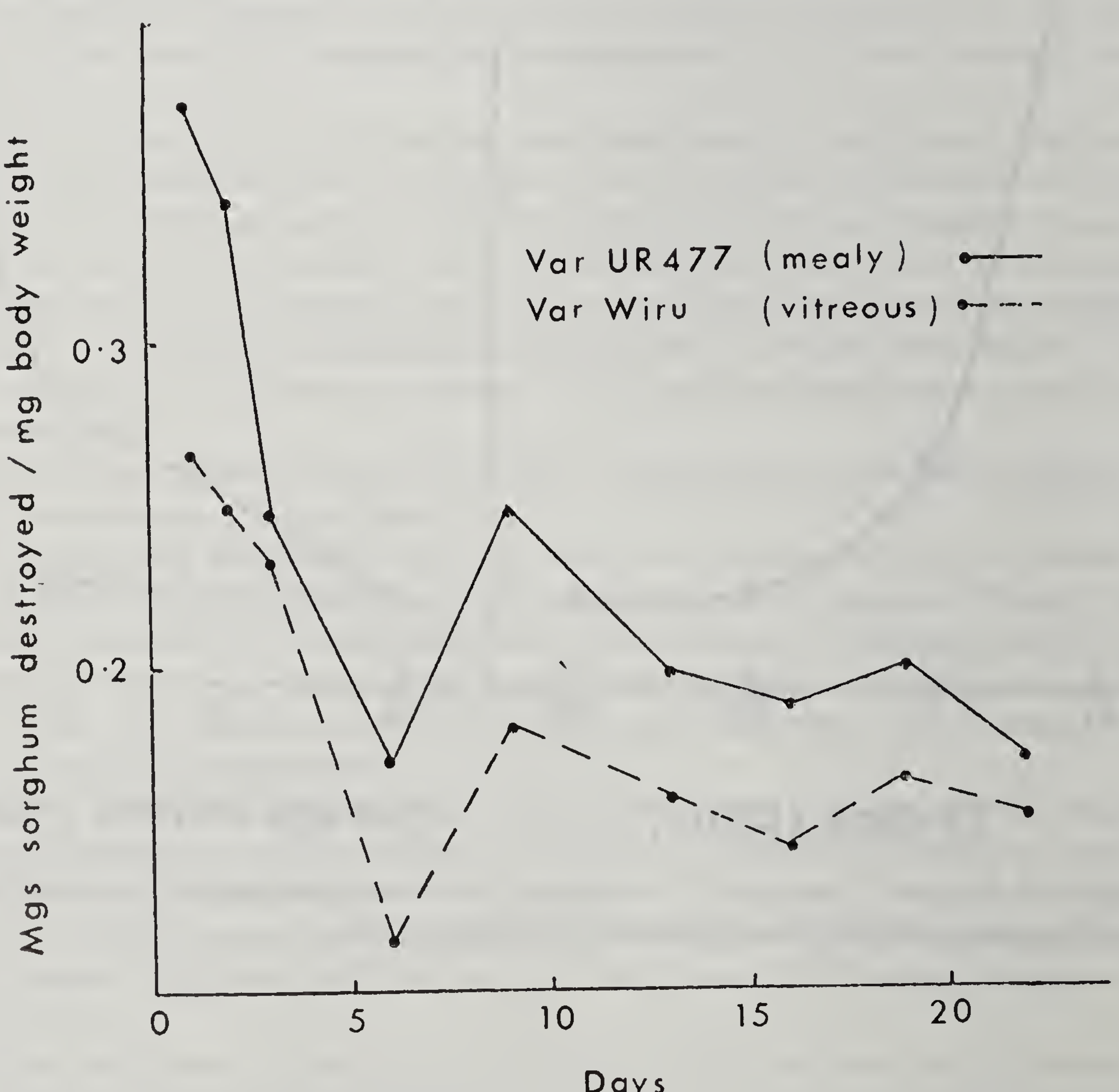

Fig. 1. Sorghum destroyed by male *Sitophilus oryzae* per day at 28°C and 70% RH.

This and the fact that hardness is only slightly affected by considerable changes in moisture content, suggests that the main factor responsible for differing susceptibilities is the hardness of the endosperm.

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SAMPLING METHODS USED IN AN INSECTICIDE FIELD TRIAL IN KENYA, TO MEASURE POPULATION LEVELS OF THREE PEST SPECIES IN STORED MAIZE

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The effectiveness of insecticide dust admixture treatments was assessed in a field trial by measuring the population level of *Sitophilus zeamais* (Motsch.) (Col. Curculionidae), *Cadra cautella* (Wlk.) (Lep. Phycitidae) and *Tribolium castaneum* (Hbst.) (Col. Tenebrionidae), together with weight of maize dust accumulated as a result of their feeding activity.

Bags of maize from different treatments were sieved on a sack sieve on each sampling occasion to remove the maize dust, insecticide dust, and that proportion of living and dead insects external to the grain or those knocked out of damaged grains.

Each sample of sievings was weighed and then divided at random using a chequer board tray sample divider. One half was weighed to check the accuracy of division. One half of each sample was then placed into a separate polythene bag and a visual count made of living adult *T. castaneum* and *S. zeamais* as soon as possible in the warehouse. The other half was placed into 30% alcohol for subsequent paraffin flotation in the laboratory. Larvae, alive at the time samples were taken, were preserved by the alcohol in a condition such that they could easily be distinguished subsequently from dead insects which were dark in colour and shrivelled.

The paraffin flotation method used was stage 4 of that described for wireworm extraction from soil samples by Cockbill, Henderson, Ross and Stapley (1). Separate tests were necessary to determine the accuracy of visual and paraffin flotation count methods used to estimate population levels. In this discussion a description of the tests carried out is given. A known number of individuals of the three species, ranging from low to moderate numbers (8-512) were placed on insect-free maize, which was then bagged and sieved. Two separate test series were carried out. Percentage recovery of living adult *T. castaneum* and *S. zeamais* was determined using the visual count method. Percentage recovery of larvae of *C. cautella* and

Table 1

Estimated recovery of insects from 200 lb. bags of maize using a sack sieve. Grain quality—reject, approximately 45% of grains damaged. Sieve mesh size 0·5 cm. Sieve angle 30°. Sieving time 10 mins/bag. Maize sievings 200 g mixed in. 5 replicates of each treatment.

No. of individuals put in	*Mean recovery % and degrees ± SE*							
	Cadra cautella		*Tribolium castaneum*				*Sitophilus zeamais*	
	mature larvae		*mature larvae*		*adults*		*adults*	
	%	*degrees ± SE*	%	*degrees ± SE*	%	*degrees ± SE*	%	*degrees ± SE*
8	91	73 ± 6·1	78	62 ± 3·2	41	40 ± 3·7	40	39 ± 5·5
16	84	66 ± 2·3	77	61 ± 4·8	45	42 ± 4·3	43	41 ± 4·0
32	91	73 ± 3·4	67	55 ± 2·2	57	49 ± 4·9	41	40 ± 4·5
64	89	71 ± 0·9	70	57 ± 3·0	54	47 ± 3·2	45	42 ± 4·1
128	89	71 ± 1·1	67	55 ± 1·1	66	54 ± 2·0	60	51 ± 2·5
256	89	71 ± 2·8	69	56 ± 1·7	62	52 ± 2·3	52	46 ± 1·0
512	89	71 ± 1·2	74	59 ± 1·5	60	51 ± 2·6	48	44 ± 2·0

T. castaneum was determined using the alcohol paraffin flotation method.

The recovery of insects by the different techniques used is fully summarised in the table of tests carried out at different population density levels.

A regression analysis of variance showed no significant difference in percentage recovery of living insects for the three species within the range of population levels studied using visual search count and paraffin flotation count techniques.

Generally there was a greater variation in percentage recovery at low population than at the higher population levels.

Percentage recovery was greater for larvae than adults.

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AN ECOLOGICAL APPROACH TO CONTROL OF INFESTATION IN GROUNDNUTS STORED IN NORTHERN NIGERIA

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Until 1963 control measures in use against pests of stored groundnuts in Northern Nigeria were basically similar to those developed by the West African Pest Infestation Survey in 1948-50 (2). Following routine fumigation against *Trogoderma granarium* Everts, this species, which does not fly, is now rarely seen on groundnuts, but *Tribolium castaneum* (Herbst) remains a serious problem. The introduction of malathion for surface spraying in 1957 (in substitution for BHC) was followed by reports of significant reductions in *Tribolium* numbers, but the development, by 1962, of a high level of resistance ($\times$ 40-50) made it necessary to consider the possibility that other factors had contributed to this reduction.

There were three factors which were undoubtedly of some importance:—

1. Elimination in Kano, by 1961, of warehouse storage of groundnuts, thereby removing an important source of cross-infestation of new crop nuts. This was followed by the concentration of open-air pyramidal stacks at special sites away from the commercial area.

2. Improvement in transportation to port, minimising the carry over of infested nuts from one season to the next.

3. Introduction of a "Special Grade" containing not less than 70% whole kernels.

The appearance, in higher numbers than in previous years, of the moth species *Cadra cautella* (Wlk.), *Plodia interpunctella* (Hübn.) and *Corcyra cephalonica* (Staint.) was generally considered to be correlated with the reduction in *Tribolium* numbers i.e. the reduction in intensity of predation of this species upon the immature stages of moths. There is, however, some evidence to suggest that the introduction of malathion, which is less effective against moths than BHC, was controlling their natural parasite, *Bracon hebetor* Say.

Clearly a re-appraisal of the situation was necessary and research effort was, therefore, directed towards an investigation of the origin of infestation in the light of changing circumstances over the past 10 years and of the ecology of the pest species in relation to the unique pyramid-shaped stacks and the physical conditions within them (3). The 172 lb. bag was taken as the sampling unit in assessing insect numbers, each bag being sieved using a large sieve, and the total number of insects present counted.

At the beginning of the intake season in November, *Tribolium* and the moth species were present in many bags of nuts delivered to Kano from buying stations; by January, 14 and 15 out of 36 bags examined were found to be infested by *Tribolium* and moths respectively (Table 1).

Table 1

Initial infestation of 36 bags of groundnuts delivered to Kano in January

Insect species	*No. of bags infested*	*Mean No. of insects per bag*	*Maximum No. of insects in a single bag*
Tribolium castaneum	14	10 (adults + larvae)	84
Moth species	15	6 (larvae)	74

In considering the ultimate fate of this infestation an experiment was first conducted to investigate the seasonal distribution of temperature within a pyramid, covered in the normal way with weatherproof tarpaulins from April to October. Afternoon surfaces temperatures, particularly above the 10th layer of bags, were generally in excess of 40°C (104°F) and in April reached 60-65°C (140-150°F). The rise in ambient temperature during March and April and the high temperatures of April and May resulted in an increase in temperature at all points within the stack though with a time lag relating to the distance from the peripheral region. The fall in ambient temperature at the onset of the rains was reflected only in the peripheral region of the stack, high temperatures (38-44°C, (100-110°F) depending upon the level) being maintained at all other points, until removal of the tarpaulins resulted in a general fall in temperature.

In order to consider insect distribution, three pyramids, constructed during the period mid-November to early January and subject to the normal routine application of contact insecticides, were broken down in February, May and October respectively. Each pyramid was broken down in the same manner so that 30 bags in comparable positions on a cross-section could be examined.

The distribution of *Tribolium* in February was rather irregular but by late May there was a tendency towards higher numbers in outer bags. Towards the end of the storage season, in early October, numbers there were very high (up to 5,000 per bag), particularly in bags whose long side had been exposed on the surface throughout the storage period (up to 9,000 per bag), whilst there were few living beetles in other bags compared with previous occasions. The increase in peripheral numbers by late May appears to be associated with the rise in ambient relative humidity and with the temperature increase in the peripheral region encouraged by tarpaulin coverage, which also results in permanent darkness from April onwards. The fact that there are no great concentrations of beetles in the internal region of the stack in May and no evidence of appreciable breeding there later lends support to the view that high temperatures are not the result of insect infestation but that heat from solar radiation is absorbed through the tarpaulins and is retained long after the fall in ambient temperature, preventing appreciable breeding in much of the stack and probably inducing outward migration from bag to bag.

Adult moths were evident at groundnut stacking areas only until April, and no living larvae were sieved from bags in May and October, suggesting that moth infestation is curtailed as a result of the presence of tarpaulins from April onwards. Published data on the physical limits of *Cadra cautella* (1) suggest that high temperature and low relative humidity are probably the major factors responsible for the elimination of moth infestation. Evidence that there is some breeding of moths in the centre of pyramids early in storage tends to confirm that this is not the result of restriction of adult movement by tarpaulins.

It was concluded that the internal stack temperatures restrict the multiplication of pests especially after sheeting, but that *Tribolium* increases considerably in the outer bags of the vertical sides. Physical conditions are such that this peripheral increase is probably aided by outward migration of adult beetles. It was clear, considering the origin of the infestation, that little control is achieved by the regular application of insecticides to the vertical sides of pyramids and recommendations were, therefore, made for such use of contact insecticides to be discontinued and an attempt made in the 1962/63 storage season to fumigate all pyramids as completed. The indication was that if all completed pyramids could be fumigated before mid-March there would be little danger of cross-infestation, because the level of *Tribolium* population at this time was low. Suction trap catches in the warehouses at Apapa during 1963 showed, in fact, that there was a marked decrease in *Tribolium* numbers compared with the previous year.

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PULSE BRUCHIDS OF AFRICA

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Little attention has been paid to the occurrence in the field and the general distribution in Africa of Bruchids affecting stored products. From discussions with entomologists and as a result of examination of material collected in the field in Africa it is evident that some members of the genus *Callosobruchus* have a very restricted range whilst others, particularly *C. maculatus* (F.) and *C. chinensis* (L.), have become very widespread covering the whole of the African continent.

Another species, *Callosobruchus rhodesianus* (Pic), has during the last two decades spread from its original home, in the Southern part of Africa to areas North of the equator. It is suggested that this species might possibly become the dominant stored products species in Africa unless its distribution and habits are carefully studied and steps taken to restrict its further spread.

The related species, *C. phaseolus* (Gyll.) is conversely a widespread species, but of no great economic importance although some of its hosts have been brought into cultivation.

The Bruchid beetle *Zabrotes subfasciatus* (Boh.) on the other hand, has in the last few years spread considerably, to the extent that it is now widespread in Africa and is breeding in the field on both *Phaseolus* and *Vigna* sp.,—host records which have not previously been noted. This species could become a serious pest in the field if left unchecked.

The absence of *Callosobruchus analis* (F.) from Africa is surprising especially as it breeds under conditions similar to those of *C. maculatus* a species which is most successful in the continent. *C. subinnotatus* (Pic), an indigenous species, maintains a restricted range in West Africa, although the host plant on which it feeds is widely grown.

CONTROL OF INFESTATION IN FOOD PROCESSING FACTORIES AND THEIR PRODUCTS

INSECT CONTROL IN THE FLOUR MILLING INDUSTRY IN CANADA

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Insect control practices in the flour milling industry in Canada are now firmly established as an integral part of flour production. Insect control in flour mills is necessary not only to ensure that flour is free of living or dead insects but also to maintain a continuous flow of stock through milling machinery. The production of insect-free flour is not the only concern of management, however. Flour, also, must be packaged, shipped and stored properly to protect it from insect infestation during the interval between production and consumption. Thus, the main insect problems in the flour milling industry in Canada relate to insect control in flour mills to prevent insect contamination of newly milled flour and, in warehouses, to prevent infestation of stored flour.

Flour mills provide a relatively constant, favourable environment and abundant food for stored product insects. The temperature of static cereal stocks in milling machinery ranges from 28° to 40°C, throughout the year. Maximum egg-laying rates and larval growth rates of important flour mill insects occur within this range. The moisture content of elevator boot stocks, where infestations often flourish, ranges from 14 to 17%.

Tribolium confusum J. du V. and *Cryptolestes turcicus* (Grouv.) comprise about 98% of the insects taken in samples from milling equipment. None of the insects that commonly infest stored grain in Canada are serious flour mill pests. Flour mill infestations must, therefore, start from other sources, the most important being (*a*) places in the mill where control measures have not been applied or have been ineffective; (*b*) empty sacks that have been returned to the mill; and (*c*) incoming food products used for blending purposes.

Elevator boots are probably the most important sites for the establishment and distribution of insect infestations throughout a flour mill. Boots often remain closed for several weeks unless mechanical failures make it necessary to open and clean them. Under these conditions, heavy infestations of *Tribolium* sp. and *Cryptolestes* sp. often occur and are, therefore, likely to be carried with stock moving through the boots to other mill equipment.

Because of differences in flour mill construction, production capacities, milling systems and regional locations, insect control programmes vary widely across the country. Many mills are fumigated annually to obtain complete control of insects in the buildings as well as in the milling system. In the Prairie Provinces, "freeze-outs" are carried out in some mills during cold winter weather. This is a highly effective method of insect control throughout all milling equipment as well as in the building structure itself. It is sometimes harmful to milling machinery and so is not popularly used.

Chemical and physical measures must be applied to keep infestation levels low during the intervals between general fumigations or "freeze-outs". Spot fumigations are usually applied to milling equipment every four weeks. Vacuum cleaners are used effectively to remove flour dust and floor sweepings. Residual insecticides are applied on the outside of milling equipment and on structural surfaces. Whenever necessary space sprays are used against moths.

Experiments in flour mills have shown that low vapour pressure fumigants applied in elevator boots were retained longer and were more effective against insects than high vapour pressure fumigants. The most effective treatments applied to elevator boots gave 70 to 75% control of insects compared to untreated boots. Local fumigation of elevator casings increased the control of insects in elevator boots by a further 10%. Thus, complete control of insects in elevator boots may only be approached by the concurrent fumigation of equipment and spouts associated with them. The commercial development of semi-automatic applicators for the spot fumigation of milling machinery has provided a means for increasing fumigation efficiency.

Infestations of flour stored in warehouses are more prevalent during spring and summer

than in winter. The main pest of bagged flour is *Ptinus villiger* (Reit.) which oviposits through the mesh of cotton and jute sacks. Paper sacks are less likely to become infested but adults and larvae may bore holes in them occasionally. Effective controls, directed against adults before they reach sacks, consist of DDT, lindane, malathion, methoxychlor, or pyrethrins—piperonyl butoxide, applied as sprays to the walls and floors of warehouses.

THE FATE OF THE INSECT MITE FAUNA IN A DERELICT FLOUR MILL IN THE ENGLISH MIDLANDS

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This paper summarises observations made in a roller flour mill between 1948 and 1964. Population fluctuations are discussed in relation to environmental changes caused by closure of the mill.

The fauna of the working mill. The associations found during production agreed with previous British records (3, 5, 7). Three habitat groups were distinguishable; general feeders, those associated with machinery and those associated with grain. The species comprising the machinery association were those named by Freeman (6) as characteristic of mills in moderate climates. Although 20 species were recorded, infestation during production was rarely more than light. Assessments of population density were made as suggested by Freeman (4).

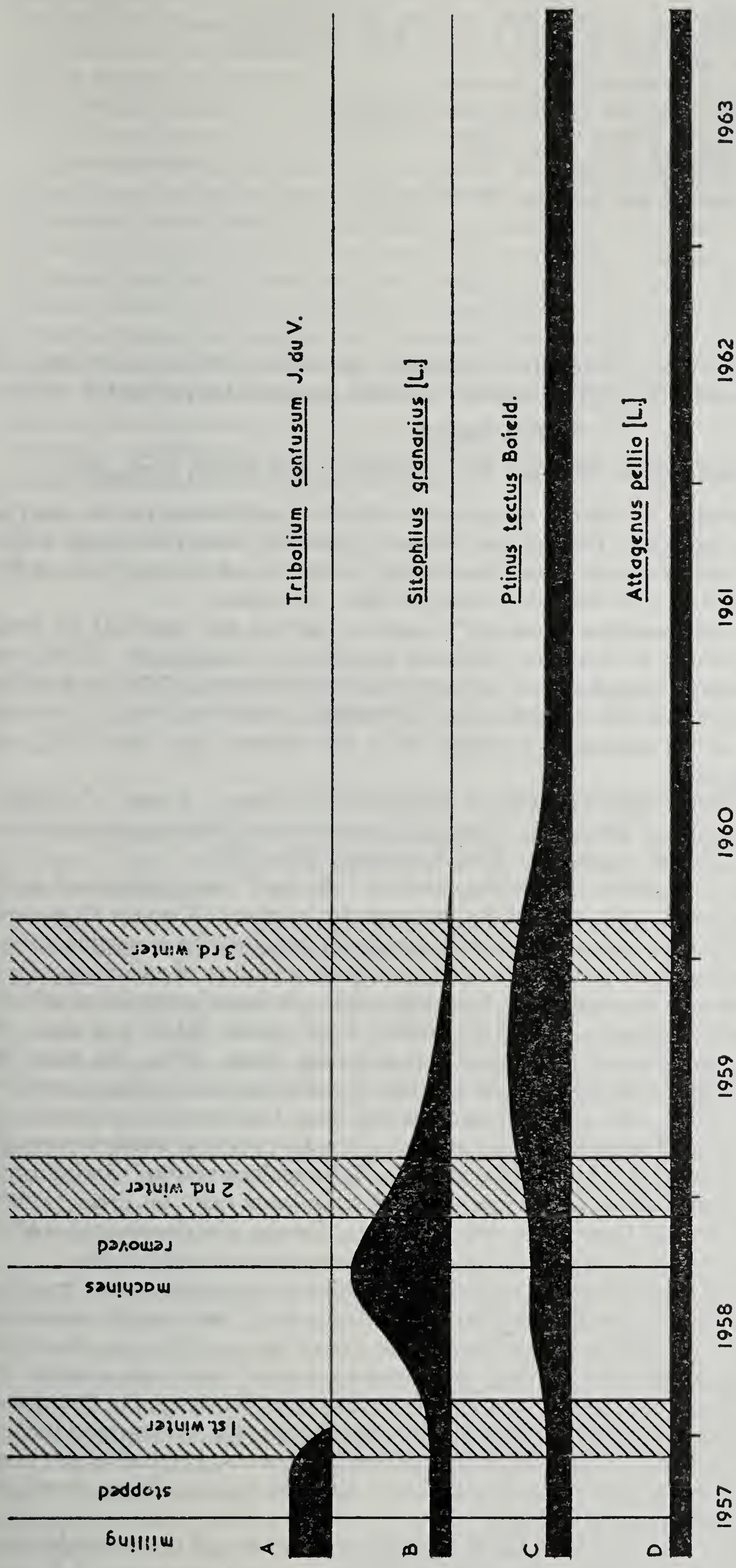
Faunal changes after closure of the mill. Milling stopped on 31st August 1957. This caused two immediate changes: insects began to multiply outside the machinery where previously cleaning had removed them and general feeders entered machinery where previously they had been excluded by high temperatures. Fig. 1 illustrates how the populations of four species fluctuated. During winter 1957-8 cold-susceptible species like *Tribolium confusum* Duv. died out (type A, fig. 1).

After closure larger populations than those discovered during production were recorded. At first, as in a similar case (8) this was due to insects being more easily found. During summer 1958 real increases occurred as species exploited undisturbed residues. *Sitophilus granarius* (L.), *Oryzaephilus surinamensis* (L.) and *Palorus ratzeburgi* Wissm. increased rapidly where whole grains of wheat were present. Other species which increased during summer 1958 were the general feeders *Acarus* sp. (recorded at the time as *Acarus siro* L.), *Ptinus tectus* Boield., *Ptinus pusillus* Sturm, *Trigonogenius globulus* Sol. and, to a lesser degree, *Tenebrio molitor* L., *Endrosis sarcitrella* (L.), and *Hofmannophila pseudospretella* (Staint.). The only cold-hardy species characteristically found in machinery, *Anagasta kühniella* (Zell.) also increased during summer 1958.

In September, 1958 the milling machinery and the foodstuffs it contained were removed. *Anagasta kühniella* was not subsequently found alive. Some other species which had at first multiplied, like the grain beetles and *Acarus* sp., exhausted their food and died out (type B Fig. 1).

In October, 1963 twelve species remained. Six had fluctuated in numbers like *Ptinus tectus* (type C Fig. 1). These were *Ptinus tectus*, *Ptinus pusillus*, *Trigonogenius globulus*, *Tenebrio molitor*, *Endrosis sarcitrella* and *Hofmannophila pseudospretella*. Six others (type D Fig. 1) had suffered little fluctuation in numbers. These were *Attagenus pellio* L., *Cryptophagus cellaris* (Scop.), *Cryptophagus saginatus* Sturm, *Scenopinus fenestralis* (L.), *Lepisma saccharina* L. and a species of Psocoptera.

Discussion. These observations show how low temperature and shortage of food caused the disappearance of the milling machinery association and the grain association. The succession of *Sitophilus granarius* by *Ptinus tectus* in wheat residues (2) was noticed and the association occurring finally was similar to that found at the end of the succession in an empty granary (1) and in dry birds' nests (9).



Population fluctuations of four species demonstrating types of response to changes caused by closure:-

A. cold susceptible

B. cold hardy but limited by rigid food requirements

C. cold hardy, able to use a wide range of foods

D. Apparently unaffected

FIG. 1. Population fluctuations of four species.

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OVIPOSITION AND DEVELOPMENT OF SOME SPECIES OF GRANIVOROUS COLEOPTERA IN PRODUCTS INTENDED FOR THE MANUFACTURE OF PASTA

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While research was being conducted to ascertain whether granivorous insects can pass alive (particularly in the egg stage) through the different phases of pasta processing, studies have also been made to discover whether these insects might oviposit and develop in the different grades of "sfarinati" intended for manufacturing the above products.

The normal commercial semolina ("semola") used in Italy as raw material for pasta making was found, on average, to have the following particle size composition: 31·6% was composed of granules passing through a sieve of apertures of 379 micron, 42·2% of granules passing through a sieve of 472 microns but refused by a 379 micron one; the 25·9% of granules passing through a sieve of 688 micron, but refused by a 472 microns one, only 0·3% was refused by a sieve 688 microns.

The measurement (length and breadth) of a significant number of eggs of *Sitophilus granarius* (L.), *S. oryzae* (L.) and of *Rhizopertha dominica* F. has shown the following average data: *S. granarius* micron 628 × 305; *S. oryzae* 570 × 274; *R. dominica* 478 × 217.

The tests concerning oviposition and development in "sfarinati" were performed on 90 samples during a 60-day period. For each of the three species involved (*S. oryzae*, *S. granarius* and *R. dominica*) 30 samples were prepared: in each sample 10 living adults of each species, if possible caught when mating, were put; the samples contained semolina of various grades in groups of five grades (plus one for control) in increasing order of size of granules as follows: (1) "Granito": a granular product obtained by milling hard wheat (64%, less than 472 microns); (2) "semola": semolina of the common commercial grade (90%, less than 688 microns); (3) "semola speciale": special semolina obtained by drawing from ordinary semolina only the largest granules (62%, less than 688 microns but none less than 472 microns); (4) "semolone": a product not used in making pasta owing to its coarseness and which is normally not sold by mills (mostly between 1114 and 688 microns); (5) "semolone vestito": an industrial product intended for further milling whose granules still have some bran on them (12·6%, larger than 1114 microns and all larger than 688 microns). During the three months of the test, all the samples were kept under optimum conditions of temperature and humidity.

The result was that both *S. oryzae* and *S. granarius* died without laying eggs in the "granito", in the normal semolina and in the special semolina; in the "semolone" both weevil species laid "free" eggs, besides several aborted eggs, but larvae born from these eggs died in a short time owing to the impossibility of sufficient feeding; in "semolone vestito" there was another step further: not only did the two weevil species abundantly lay free eggs, but several of their larvae succeeded in living and feeding for a limited time (up to twice the size of newly emerged larvae); some of them (but only of *S. oryzae*) succeeded in growing into adults, but had a size much inferior to the normal. *R. dominica* on the contrary had no difficulty in ovipositing, developing and reproducing in all tested grades of semolina.

To complete the above tests and in order to establish whether weevil larvae might develop in small granules, some kernels of durum wheat with an internal infestation of *S. oryzae*

were chipped out by hand in such a way as to be sure to leave a living egg within each granule. The 10 resulting granules were kept under observation for 45 days; no egg development occurred in 5 granules, while in each of the 5 others one larva developed regularly: these larvae, however, died in a more or less short time after emergence from granules, with the exception of one larva, which succeeded in developing into a small, distorted and incomplete pupa, that survived a few days.

In conclusion, "sfarinati" granulometry and egg micrometry showed that in semolina normally used in Italy in pasta making, and even more so, in "graniti" or in flour, the majority of granules cannot hold *S. oryzae* and *S. granarius* eggs, and therefore granules with a sound egg within them (and even more so, a living larva of these species) are unlikely to be found in the above semolina; in practice, one could say that this is impossible. On the other hand it has been shown that in the "sfarinati" (uncompressed "graniti" and semolina) normally used in making pasta, oviposition and therefore development and reproduction of weevils does not take place, while this normally occurs for *R. dominica*.

It is therefore considered as proved that in "sfarinati" normally used in pasta manufacturing an infestation of *S. oryzae* or *S. granarius* cannot take place with character of continuity and capability of reproduction and development from egg to egg, while the same thing is possible as far as *R. dominica* is concerned.

FOOD-HANDLING PREMISES IN BRITAIN AS AN ECOLOGICAL NICHE FOR *DERMESTES* (COLEOPTERA, DERMESTIDAE)

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Only four species of the genus *Dermestes*, namely *D. lardarius* L., *D. maculatus* Deg., *D. peruvianus* Cast., and *D. haemorrhoidalis* Kust. are found with regularity in food-handling premises in Britain.

Food-handling premises include factories processing food materials for animal and human consumption, retail shops handling meats and pet-foods, cafés and canteens, and domestic premises.

Whilst all four species are established in Britain there is a continuing process of introduction through imported foodstuffs. *D. maculatus* arrives on bones and hides, *D. lardarius* and *D. peruvianus* on fish meals, and *D. haemorrhoidalis* is brought in on sheep skins and bone meal.

Within Britain infestation appears to spread mainly by the insects being carried from one place to another in goods or equipment, though there is evidence from light-trap captures that flight of the adult beetles plays some part. It is probable that birds' nests and bat roosts form natural reservoirs for the species in buildings from which infestation may spread.

What are the main ecological requirements of these four species of *Dermestes* and how do food-handling premises meet them?

1. *A need for warm conditions.* *D. lardarius*, *D. peruvianus* and *D. haemorrhoidalis* breed most rapidly at around 28°C, and *D. maculatus* at the slightly higher figure of 32°C. In food-handling premises these temperature conditions are found in the vicinity of machinery, cooking ranges and similar equipment, and near refrigerators.
2. *An adequate supply of a suitable food medium.* All the species thrive on materials containing protein of animal origin, and in food-handling premises such as fish meal factories, butchers' shops and canteens, suitable food abounds in the form of stock or spillage.
3. *A source of moisture.* The adult females of these species produce a greater number of eggs when they have access to water. Defects in design, construction, equipment and cleaning methods in many premises provide a constant supply of water for the beetles.
4. *Minimum disturbance of the infesting population.* The breeding sites of *Dermestes* in food-handling premises are located behind false walls, beneath built-in equipment, such as cooking

stoves, hotplates and refrigerators, and under linoleum used as a floor covering in many premises.

Distribution. *D. maculatus* appears to be confined to manufacturing premises and no records have yet been found of its occurrence in canteens and similar premises. *D. lardarius* is found throughout Britain and is the most common species. However, since the early 1950's an increasing number of infestations of *D. peruvianus* and *D. haemorrhoidalis* in food-handling premises have been found, and these two species appear to be relatively common (1).

Economic significance. Though material losses are probably not great, loss of trade reputation resulting from the discovery of beetles in food by the public can be serious, especially to a small trader. Structural damage particularly to woodwork can sometimes be caused by the boring habit of the larvae immediately prior to pupation.

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PROBLEMS OF THE FOOD MANUFACTURER IN RELATION TO INSECT DEVELOPMENT IN THE GOODS THAT REACH THE CONSUMER

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In the Cocoa and Chocolate Industry the risk due to insect damage of appreciable loss of foodstuffs has virtually disappeared in this country. Nevertheless the Food and Drugs Act, 1955 makes it unlawful to sell foodstuffs not of the quality demanded which has resulted in an increasing tendency for members of the public to take their "grubby" purchases to Public Health Departments.

In 1960 about one person in 200 of those finding live insects in their chocolate took this action. In 1935, although the number of people complaining was about the same as in 1960 no one went to a Public Health Department. This trend is causing apprehension among manufacturers, especially the risk of the complaint being given wide adverse publicity in reports of legal proceedings.

The proportion of total production affected by insects may be very small. Thus the "infestation index" for one company (number of complaints per 1,000 tons chocolate sold) rose steadily from 21 in 1921 to 180 in 1935; by 1945 after a period when any chocolate available was rapidly sold, the index was only 2; by 1955 the index was back to 43 and by 1960 to 100. Some of this increase may be explained by a greater willingness of people to complain.

The complaint is generally directed at the manufacturer because prepacking associates his name with the defective food. This is despite the fact that over 30 years study has shown that in over 99% of the cases the infection took place after the goods left the manufacturer's control. This study also shows that the main offender is *Ephestia elutella* (Hübn). One of the principal pieces of evidence of infestation originating outside the factory is that moths trapped in the factory are generally in the proportion 95 *Cadra cautella* (Walk.) (originating from the raw cocoa beans) to 5 *Ephestia elutella* and in the reverse proportion for those returned by the public. Complaints come back in a characteristic pattern: a main peak in early October and a smaller one in January, with the trough in May to July.

Beetles, particularly *Ptinus tectus* Boield. are causing a steady but slow increase in their proportion of complaints from 13% in 1921 to 21% in 1963 and are commoner than *Ephestia elutella* in complaints from the more northerly areas of Britain.

Since the female *Ephestia elutella* moths lay eggs at random most of the original infection occurs when the newly hatched larvae are wandering, which they may do up to three feet away from the place where the eggs were laid. They can get through holes 0·007 ins. diameter but they do not appear to be able to detect suitable foodstuffs at a distance and do not prefer one type of chocolate to another although development is quicker on chocolate containing nuts and on dark rather than milk chocolate.

It is extremely difficult to produce an economical wrap or container proof against entry

of insects. Although foil used to wrap chocolate blocks contains holes larger than the 0·007 ins. diameter which the larvae can enter they do not readily find them and tend to enter through the folds. Heat sealed folds can be up to 90% effective if carefully done and provided that subsequent handling does not damage the foil. This usually means an additional paper wrap to protect the foil. The 10% failure is mainly due to the seal opening where the foil is folded before the adhesive has time to set.

Larvae enter tins with push on lids sealed with adhesive tape through the tunnel formed by the seam of the body of the tin under the tape and lid. A press in lid fails to the extent of 1 in 300 and strangely enough a tin with a paper or foil diaphragm under the lid quite often fails more frequently than the press-on lidded one without the diaphragm.

There has been little success with wrapping material incorporating insecticides and cold welding of foil instead of heat sealing cannot yet handle foil as thin as is economical to use. On the other hand goods wrapped in five sheets of paper wrapped envelope fashion with the folds not all in the same position have very good protection.

It seems very difficult therefore to guarantee that no moth larvae are going to get into packaged products if they are given the chance. What can be done about preventing the larvae appearing where they can menace such goods?

Even ignoring the risk of increasing the traces of chemicals present in foodstuffs, insecticides offer no solution to this problem because it is so diffuse. The general use of prepackaging and the substitution of new premises for small shops will have some temporary advantageous effect, but in the long run the solution to the problem seems to rest on a higher standard of hygiene from everyone.

PRACTICAL METHODS FOR THE PROTECTION OF PROCESSED FOODSTUFFS FROM INFESTATION DURING MANUFACTURE AND STORAGE

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The presence of insects in a food manufacturer's commodity may seriously affect his reputation and lead to litigation. He is concerned with a very large number of species of domestic and public health importance in addition to pests of stored products, as well as accidental intruders. The preventive and control measures employed may be placed under three headings.

I. *Physical.* Maintenance of good standards of hygiene, lighting, ventilation, temperature control and humidity must receive particular attention. Design of machinery and methods of storage should allow ready inspection, isolation and treatment if necessary.

In general, the use of insect traps is of value only as a guide to the number of insects present, because trapped insects may have already laid eggs. Suction traps and adhesive tapes are used to record the numbers of *Plodia interpunctella* in Australian dried fruit stores and *Ephestia elutella* and *Lasioderma serricorne* in tobacco factories and bonds. Electrified traps employing a high voltage grid and U.V. light have been commercially developed and are said to be effective in reducing numbers of Diptera, including houseflies and blowflies in meat packing factories. Insufficient information is yet available to assess their performance in the presence of highly attractive foods and against stored products moths and other insects which may not be attracted to the particular wavelength of light emitted.

Among physical measures is included the use of mechanical methods for the high speed disintegration of insects, but machines designed for this are often placed incorrectly and permit re-infestation of food before packing.

II. *Chemical.* These include fumigation and the use of contact insecticides including aerosols, residual insecticides and poison baits. Recent restrictions on the use of certain chlorinated hydrocarbons in Britain have limited the food manufacturer or servicing company in the choice of insecticides which they can use with safety near foodstuffs. The latter requires a product with prolonged residual effect, particularly for cockroach and ant control. The organo-phosphorus insecticides, including malathion and diazinon, are being used in increasing

quantities particularly against *Blattella germanica* which is showing resistance to chlorinated insecticides in Britain and elsewhere.

Synergised pyrethrins are being used in increasing amounts in food undertakings because of their safety and efficiency. In addition to their conventional use, electrically operated pressure packs have been developed to discharge 100 mg. aerosol every 15 minutes for about 35 days. In practice, the repellent property of pyrethrins is probably more important than the knockdown and lethal effect on flying insects. The machines are particularly applicable to the dairy and catering industries.

Their effect is being assessed against the Mediterranean flour moth (*Anagasta kühniella*) in a flour mill and against *Ephestia* spp. in confectionery undertakings. In a small store, artificially and heavily infested with these insects, the number of free flying moths has been reduced by over 90%, by operating the machine only 4-8 hrs. daily.

Poison baits have not been fully evaluated in Britain. The author agrees with Pence (4) that decachloro-octahydro-1, 3, 4,-methano-2H-cyclobuta (cd) pentalen-2-one, is effective against *Blattella*. The effect of applying this combined with a sex attractant is worth investigating; Yamamoto (5) has reported that males of this species are highly attracted to material extracted from females.

III. *Insect Proofing of Food Containers.* Insects found in processed food may have entered the commodity after it has left the manufacturer and whilst it is in the wholesaler's premises, shop, or even in the home. The normal food cartons employing waxed or glassine liners within a printed carton board packet, offer little protection from insect penetration and first instar larvae readily enter. The only complete physical method of protection is the soldered tin, which is often too costly except for the most expensive commodities.

In 1960, Brooke (1) described his results obtained with slurry coatings containing a mixture of pyrethrins and piperonyl butoxide applied to the surface of food containers. Other products have subsequently been developed containing the same insecticide dissolved in lacquers and waxes; these have proved to be effective and safe in preventing insect penetration into processed foodstuffs (2, 3). The lacquer, applied by the carton board printer before the board is cut up, replaces the usual over-printing varnish and acts as a repellent in addition to having a lethal effect against insects. Speed of its action is of great importance. Slow acting insecticides with little repellent effect are unsuitable for use on food packets which are not completely sealed as they may permit insects to enter. The presence of dead or live insects is equally obnoxious to the consumer.

A mixture of pyrethrins and piperonyl butoxide dissolved in paraffin wax is also used in liners for outer food containers to protect packets within, but protection is lost once these are removed.

The development of multi-wall paper sacks in place of jute has afforded some measure of protection from insect penetration. Insecticidal waxed paper strips used in place of the existing closures have been found in practice, to prevent insects entering through stitch holes.

Application of insecticide as a lacquer or waxed strip closure should entail no toxic hazard or taint the food. The product is not in direct contact with the commodity and with lacquer, there is negligible penetration of the carton board. In any event, products containing these two substances can be used safely near foodstuffs. Results of field experiments and commercial use in Britain and the tropics have indicated protection for 12 months after packing. The additional cost of using insect-proofed containers may limit application to the more expensive commodities. At present, treatment including application, adds approximately 0·2 pence per sq. ft. (2¼d. per sq. m.) of carton board and about one penny to a 56 lb. paper sack.

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CONTROL BY CHEMICAL AND BIOLOGICAL AGENTS

THE RESPONSE OF STORED PRODUCT INSECTS TO FUMIGANTS APPLIED UNDER REDUCED PRESSURE

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The response of insects to the reduced pressures used in vacuum fumigation is complex. Monro (1) showed that *Tenebroides mauritanicus* (L.) and *Tenebrio molitor* L. were more susceptible to methyl bromide when exposed in air at 100 mm than at 30-50 mm Hg. Monro *et al.* (2) found that CO_2 expiration of *T. mauritanicus* larvae was greater at 100 mm than at 35 mm. In the present study larvae and adults of *T. mauritanicus*, adults of *Sitophilus granarius* L. and larvae of *T. molitor* were exposed at 35 and at 100 mm for 90 minutes at 25°C to some or all of the materials shown in figure 1. Different dosages were applied under these conditions until

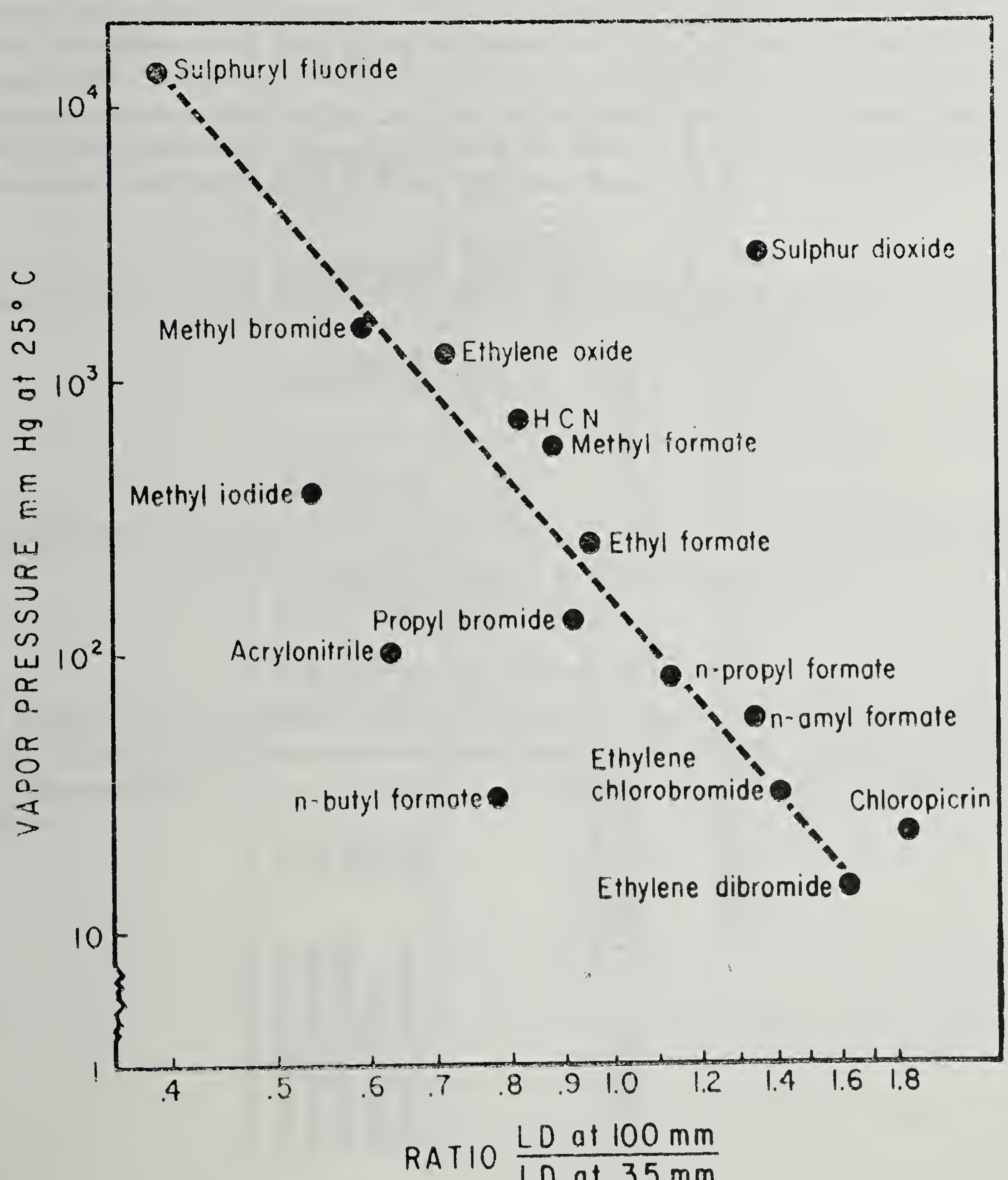

Fig. 1. Logarithmic plot of the Ratio LD_{50} at 100 mm/LD_{50} at 35 mm against the vapour pressure at 25°C of 16 compounds used against the larvae of *T. mauritanicus*.

TABLE 1

Responses of insects to alkyl formates in vacuum fumigation (90 minutes exposure at 25°C)

LD_{50} mg/l at 35 and 100 mm Hg pressure

Fumigant	*Vapour pressure at 25°C mm Hg*	*T. mauritanicus*						*S. granarius adults*			*T. molitor larvae*		
		larvae			*adults*								
		(a) 35 mm	*(b) 100 mm*	*Ratio b/a*	*(a) 35 mm*	*(b) 100 mm*	*Ratio b/a*	*(a) 35 mm*	*(b) 100 mm*	*Ratio b/a*	*(a) 35 mm*	*(b) 100 mm*	*Ratio b/a*
Methyl formate	590	10·3	9·2	·89	10·2	9·0	·88	4·4	5·0	1·14	15·0	8·4	·56
Ethyl formate	255	12·7	12·2	·96	9·1	8·8	·97	6·8	5·8	·85	14·0	13·8	·98
n-propyl formate	83	10·5	12·0	1·14	9·2	10·9	1·18	9·6	11·8	1·23	12·5	13·9	1·11
n-butyl formate	28	53·3	41·0	·77	19·7	17·8	·90	13·4	11·8	·88	17·9	20·9	1·14
n-amyl formate	15	24·7	33·3	1·35	17·3	26·9	1·55	6·4	11·9	1·86	34·5	38·1	1·10

the LD_{50} at each pressure could be established within 95 per cent confidence limits. Table 1 shows the results of these experiments with a homologous series of alkyl formates. In order to provide a common basis for comparison of the responses the following arbitrary ratio was adopted:—

$$\frac{LD_{50} \text{ at } 100 \text{ mm}}{LD_{50} \text{ at } \ \ 35 \text{ mm}}$$

Fig. 1 shows 16 such ratios, derived from the results with volatile chemicals used on the larvae of *T. mauritanicus*, plotted against the vapour pressure of each compound at 25°C. It is seen that the general tendency is for the insects to be progressively more susceptible at 35 mm than at 100 mm as the vapour pressure of the compounds decreases.

Larvae of *T. mauritanicus* were taken at different intervals subsequent to fumigation with ethylene dibromide with 3 mg/l at 35 mm and 100 mm pressure, other conditions as above. Residual ethylene dibromide in the larvae was extracted with petroleum ether and analysed by gas chromatography. The results of this analysis in terms of weight of fumigant per body weight of insect show that the ethylene dibromide persists in greater amounts in the insects fumigated at 35 mm.

It is clear that the vapour pressure of a fumigant has an important influence on the responses of insects fumigated at different pressures. The results amplify the earlier finding with methyl bromide alone (1) and show that in vacuum fumigation low boiling fumigants may exert greater toxic effect at pressures at which the rate of respiration is not reduced. On the other hand fumigants with low vapour pressures, such as ethylene dibromide, may exert greater toxic effect at lower pressures although the respiration of the insects is depressed. This effect appears to be due to the fact that at the lower pressure a greater amount of high boiling fumigant gains access to and persists in the insect at 35 mm than at 100 mm, and this provides a greater residual fumigant action following treatment.

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THE TOXICITY OF FUMIGANTS TO THE EGGS OF *TRIBOLIUM CONFUSUM* DUVAL (COLEOPTERA, TENEBRIONIDAE)

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The study of four fumigants, ethylene dibromide, ethylene dichloride, methyl bromide and sulphuryl fluoride has been made in relation to their toxic effect on the eggs of *Tribolium confusum*. Susceptibility to these fumigants has been found to vary with degree of embryonic development.

QUARANTINE FUMIGATION OF IMPORTED COMMODITIES WITH METHYL BROMIDE OR ETHYLENE OXIDE MIXTURE UNDER TARPAULINS

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Fumigation with methyl bromide under tarpaulins (or gas-proof sheets) has had wide, practical use for over 20 years. In the United States, it probably was first tried on imported commodities as an emergency quarantine measure but in recent years it has become an almost standard quarantine treatment for some insect infested, imported fruits and other cargo. Tarpaulin fumigation has often been urgently needed in quarantine due to the limited capacity of fixed fumigation facilities and the increased volume of cargo. Ethylene oxide 10%-carbon dioxide 90% (Carboxide) has also had quarantine use under tarpaulin during the past year on inert cargo.

The main advantages of tarpaulin fumigation in quarantine are: (*a*) it is economical, (*b*) it reduces risk of pest spread by treatment at ship's pier, (*c*) it is easily adaptable to many situations, and (*d*) it allows very large amounts of cargo intransit to be treated expeditiously. Reliable application is possible, mainly by use of rapid thermal-conductivity analysers, so fumigant dosage, distribution and losses during fumigation can be determined and immediately corrected, if necessary, to ensure high efficiency. Forced circulation with fans or blowers—just at the start—to provide uniform space distribution is extremely important. No subsequent stratification of either fumigant has been noted in 72-hr. fumigations. Dosage errors sometimes occur. Under-dosages can be corrected immediately by the addition of more gas. Small over-dosages are usually not objectionable with inert commodities but may be important with fruit, etc., in which case exposure is shortened but only enough to correct the concentration-time factors to ensure effective treatment. Six-gauge (0·006″) polyethylene sheets are commonly used as tarpaulins indoors, but plastic-coated nylon is preferred for long, outdoor fumigations. With Carboxide, considerable slack is left in the tarpaulins (or a "bleeding" tube installed) so that large dosages can be applied without substantial gas loss.

Extra precautions for personnel safety are required in tarpaulin fumigation, especially indoors. Methyl bromide has no warning odor at low concentrations, nor any specific antidote. Leakage into the working areas may be detected with halide detector lamps, but readings near the U.S. maximum acceptable concentration for industrial exposure of 20 ppm are often questionable. More sensitive detectors are needed. In tests since 1962 a methyl bromide detector tube (stain reaction-Kitagawa) has appeared promising for practical use (range near 5 to 500 ppm). Heseltine found a similar type satisfactory. An ethylene oxide tube (Kitagawa) has also appeared promising for Carboxide (range near 10 to 35,000 ppm—U.S. maximum acceptable 50 ppm). With this high range, the tube also appeared practical for measuring ethylene oxide concentrations under the tarpaulin in conjunction with T/C analysis. Completed tarpaulin fumigations made indoors can be ventilated with a portable centrifugal blower equipped with a large, flexible tube extending to the outside. Recently a 1900-cfm blower reduced methyl bromide concentrations in a 7,000 cu. ft. fruit fumigation from 35 to about 1 oz. per 1,000 cu. ft. in 20 minutes.

Mention of trademarked products herein does not necessarily imply USDA endorsement.

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THE FUMIGATION WITH METHYL BROMIDE OF MALT PACKED IN BAGS WITH POLYTHENE LINERS

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The malt packed in hundredweight jute bags with polythene liners 0·002 in. thick (0·05 mm) was fumigated in barges, using a dosage of 3lb. methyl bromide per 1,000 cu ft. (48 g/cu.M). The barges had only a single hold but two hatch openings—a main one and a smaller one forward. The forward part of the hold was usually more heavily loaded than the remainder with bags right up to the hatchboards whereas elsewhere the bags were no higher than deck level. The fumigant was applied through copper piping fitted with atomising jets using a separate piping system for the forward part of the hold. During the course of the fumigations gas samples were drawn into evacuated flasks containing monoethanolamine and the methyl bromide subsequently determined by Volhard's method.

To test the possibility of increasing the efficiency of the fumigation by punching holes in the polythene liners, pairs of bags were selected side by side and a gas sampling capillary placed in each. One bag of each pair was then punched six times with a board carrying six 2″ nails.

Results obtained. The results are summarised in the Table. The figures take no account of CXT product during the airing period which might have amounted to an extra 20 mg. h/l. In the free space the maximum CXT product was 1,000 and the average 550 mg. h/l.

Discussion. The results in the forward part of the hold are markedly inferior to those in the main part in every case except test 2 where in place of the usual 125 tons only 75 tons was carried and there was ample space above the bags over the whole area of the hold. As to be expected, the punching of holes usually resulted in greatly increased CXT products. In the two cases where the figure was lower in the punched bag the figure in the normal bag was high, suggesting that it was already damaged or loosely tied. Preliminary tests by the maltster showed that the increased uptake of moisture in punched bags on storage would probably not be sufficient to make the method unacceptable.

Conclusions. Work by Burns Brown and co-workers has given the following results for the mortality of *Trogoderma granarium* larvae exposed to various concentration time products of methyl bromide:—

at 10°C 250 mg. h/l gives a mortality of 99·6%, 200 mg. h/l one of 98%

at 15°C 200 mg. h/l gives a mortality of 99·9% or higher, 160 mg. h/l one of 99·4%

From these figures it is concluded that in the circumstances described, a dosage 3lb./1,000 cu. ft. for 48 hours is effective against *T. granarium* at 15°C and above and possibly above10°C provided that the barge is suitably stowed to facilitate even distribution of fumigant over the surface of the cargo. Below 10°C some survival would be possible. Punching holes in the bags is not of itself sufficient to offset overstowage and low temperature.

Concentration Time Products in Milligram Hours per Litre Inside Bags

Test No.	1	2	3	4	5	6
Month	Feb.	Feb.	Mar.	May	June	Aug.
Air temp.	1°C	4°C	10°C	15°C	not taken	17°C
Wt. of Malt in tons	125	75	75	125	125	125
CXT Product in	75	180	40	170	115	100
forward part of hold			95H	195H	140H	150H
CXT Product in	100	190	180	325	335	215
main part of hold			285H	425H	290H	275H
	90		100	310	550	275
			155H	265H		315

"H" denotes that the bag had been punched with holes.

Test No. 3 was done in a barge of capacity 6300 cu. ft. (180 cu.m) and all the others in one of capacity 9300 cu. ft. (260 cu.m).

FUMIGATION AIMED AT COMPLETE MORTALITY

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In the fumigation of stored produce it is often assumed that for any given set of conditions and irrespective of the number of insects present there is a level of treatment, which, if exceeded ensures a complete kill but if not reached allows survivors. This is an over-simplification. In this paper we show how dosage estimation can be considered in terms of probability rather than certainty of complete kill.

A dosage level for 100% kill cannot be estimated from observations of the dosage-mortality responses in samples. It is customary to provide dosage estimates for some level of kill, such as 99·9%, which has been considered near enough to 100% for practical purposes.

If a treatment expected to give 99·9% kill in an infinitely large population is applied to a number of samples of 1,000 insects we expect to obtain 100% kill in some of these samples whilst others have one survivor and some two or more. If these survivors are distributed at random we can use the Poisson distribution to calculate probabilities of observing 0 or 1 or 2 or more survivors in a sample.

Let us consider the simple case of a consignment of 1,000 bags of produce, each carrying 100 insects fumigated under conditions allowing a perfect distribution of the gas so that a level of treatment estimated to kill 99·9% is obtained at all points. We can expect one or more insects to survive in about 95 of the 1,000 bags. Detection of survival at this low level is obviously of extreme difficulty and its importance in various circumstances is not known with any certainty.

If the initial number of insects per bag is 1,000 instead of 100 we can calculate that we should expect 1 or more survivors in about two thirds of the consignment of bags and 2 or more survivors in a quarter of them. If this is unacceptable the dose must be increased to give a result closer to a complete kill.

The probabilities of survivors from treatments at increased levels of dose can be calculated if it is accepted that the laboratory toxicity data give a straight probit kill/log dose regression line which can be extrapolated to high probit kills. Applying typical data for methyl bromide obtained at the Pest Infestation Laboratory to the example just considered it can be estimated that an increase of dose by the modest factor of 1·25 will raise the expected percentage kill from 99·9 (probit 8·1) to 99·9978 (probit 9·1) so that in our consignment of 1,000 bags each carrying 1,000 insects we can expect survival in only about 22 bags. Increase of the original dose by a factor of 1·6 will, on this basis, result in a complete kill throughout the consignment of 1,000 bags about 85 times out of 100 treatments.

In normal fumigation practice the effects of uneven initial distribution of insects between bags and of uneven treatment must be taken into account.

There is a clear need for experimental evaluation of the validity and reliability of the types of estimate proposed in this paper.

RECORDING THE SUSCEPTIBILITY LEVELS OF CURRENT STORED PRODUCT PEST POPULATIONS TO CURRENT INSECTICIDES

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The Macdonald College Test Kit consists of filter paper substrates impregnated with known amounts of insecticide distributed in acetone by means of calibrated syringes; paper cups, three inches deep by two inches in diameter and fitted glass rings. The cups serve as pretreatment, treatment and post-treatment cages. The treatment cages are lined on the bottom and sides with treated paper and the insect confined by greased rings fitted near the tops of the cups and perforated covers.

p-p' DDT; dieldrin; aldrin; heptachlor; and lindane have been tested against *Tribolium*

confusum (Duv.) (two strains); *T. castaneum* (Herbst) (one strain); *Cryptolestes ferrugineus* (Steph.) (one strain); *Sitophilus granarius* (L.) (four strains). The different strains came from Montreal, Quebec, Macdonald College, Quebec, Guelph, London and Ottawa in Ontario; Winnipeg, Manitoba, and Edmonton, Alberta. The work is continuing both at Macdonald College and at other stations.

After a pretreatment conditioning period in holding cages lots of 50 test insects are exposed to the treated paper inside exposure cages for from two to twenty-four hours at each of six concentrations selected on a basis of preliminary testing. Mortality records are after twenty-four hours. Treatment cages are discarded. Each test is replicated four or five times and the log-dosage regression line drawn and calculated by the method of Finney (1). Temperature and humidity conditions during tests were carefully regulated. Detailed instructions accompany test kits sent out.

A sample of the thirty-three fully completed tests to date is shown below.

No.	*Name of Insect*	*Strain*	*Insecticide*	*LD 50 (gms *per 100 ml. acetone*
1	*Tribolium confusum* (Duv.)	Winnipeg	DDT	0·045-ne.
2	*T. confusum*	Macdonald	DDT	1·116
3	*Sitophilus granarius* (L.)	Guelph	DDT	0·037
4	*S. granarius* (L.)	London, Normal	DDT	0·046
5	*S. granarius* (L.)	Macdonald	DDT	0·095
6	*S. granarius* (L.)	Winnipeg	DDT	0·230
7	*S. granarius* (L.)	Guelph	dieldrin	0·048
8	*S. granarius* (L.)	Winnipeg	dieldrin	0·095
9	*Oryzaephilus surinamensis* (L.)	Macdonald	lindane	0·592

*gms per 100 ml. of soln used at 0·097 ml. soln per square inch to impregnate paper.

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THE ONSET OF INSECTICIDE RESISTANCE AMONG FIELD STRAINS OF STORED-PRODUCT INSECTS

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Resistance has not developed so rapidly among stored-product insects as among public health and agricultural insects. This is in spite of the frequent use of relatively persistent contact insecticides such as lindane, malathion, and DDT. Several factors have probably contributed to this delay. For instance, most stored-product insects have fewer generations per annum than public health species. The commonest applications of contact insecticides are often superficial and incomplete on sacks and building surfaces, so that selection pressure is not high. Treatments rarely cover all stores in a locality and dilution of strains with incipient resistance by susceptible insects from neighbouring stores, farms, markets, etc. is common. Again goods are frequently moved in and out of stores so that bulks of treated produce, together with their insect fauna, are replaced by fresh goods carrying susceptible insects. Finally, fumigation can eliminate a population in process of acquiring resistance to a contact insecticide. Marked resistance to fumigants has not yet been observed.

The highest levels of resistance resulting from laboratory selection are as follows:

Species	*Insecticide*	*Technique*	*Generations treated*	*R factor*	*Author*
S. granarius (L.)	Pyrethrins	Topical	26	52	Lloyd and Parkin (5)
S. granarius (L.)	Me bromide	Fumigation	29	5·5	Monro *et al.* (7)
S. zeamais (Mots.)	Lindane	In food	30	12	Parkin and Forster (8)
T. confusum J. du V.	DDT	In food	10–15	2–8	Maeda (6)
T. confusum J. du V.	Me formate	Fumigation	35	3	Anon. (1)
T. castaneum Hbst.	DDT	In food	4	12	Dyte and Blackman (3)

Resistance of *S. granarius* to DDT and of *O. surinamensis* (L.) to carbaryl has also been reported but without resistance factors.

Since 1959, strains suspected of resistance to contact insecticides in various parts of the world have been tested by the author, using a simple technique of exposure to a graded series of concentrations of insecticide applied as a dust to grain and determining percentage kill after 3 days exposure at 25°C and 70% R.H. Thirty-three strains have been received and 25 tested. The highest factors of resistance for each species in comparison with strains considered susceptible are as follows:

Species	*Strain*	*Origin*	*Insecticide*	*R factor*
S. granarius	S. Africa I	Barley	Lindane	2·5
S. zeamais	Trinidad I	Rice (Siam)	Lindane	7·9
S. oryzae	Trinidad II	Rice	Lindane	13·2
O. surinamensis	Kenya VI	Maize	Lindane	2·7
T. castaneum	Nigeria I-VI	Groundnuts	Malathion	40–60

The *T. castaneum* were collected in Kano, N. Nigeria, where a malathion water-dispersible powder had been used for three years in the groundnut storage area. Other strains of *T. castaneum* collected from cowpeas, maize or tobacco at Ibadan had factors for malathion resistance of 10–16. Champ and Cribb (2) report a resistance factor of × 85 to lindane for *S. oryzae* from hybrid sorghum seed. Because of a difference in technique, this value cannot be compared with the P.I.L. factors but clearly shows considerable resistance. Finally, slight field resistance by *O. mercator* to malathion (4) and *Cadra cautella* (Walk.) to pyrethrins (Henderson, unpublished) are also known.

Eight species of stored product insects have now shown resistance to eight insecticides and the international specification and co-ordination of test techniques and collection of data on levels of tolerance of susceptible and resistant strains throughout the world are urgently needed.

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POSSIBILITIES OF BIOLOGICAL CONTROL OF STORED PRODUCTS INSECTS

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Will biological control of insects be useful in the stored products field: does it approach the ideal—a cheap, efficient, insect-specific method? Certainly most biological agents are insect-specific and involve no taints or hazards. However, they tend to be too specific, each killing possibly only one species in a mixed population. Inactivity against predatory and parasitic insects is unimportant, because these are usually insignificant in stored products. Occasionally natural epidemics have given good, albeit late, control at absolutely no cost, e.g., *Bacillus thuringiensis* Berliner in *Cadra cautella* (Walker) on maize recently in Kenya.

Micro-organisms offer more promise of success than predatory or parasitic insects. They can either be seeded in a pest population or applied regularly as microbial insecticides.

Seeding leaves the insect to do the work of disseminating the pathogen. Success depends mainly on the infectivity of the initial seed and on the subsequent transmission of the disease from insect to insect, e.g., a hardy initial seed with subsequent transovarial transmission. Viruses and Protozoa produced in vivo and seeded may reduce residual populations of pests in individual stores or the general population in a whole area, particularly in warm countries. It is believed that *Triboliocystis garnhami* Dissanaike is now curbing populations of *Tribolium* in the Gambia.

For routine use as a microbial insecticide, an organism must have a hardy, long-lived, dormant stage, capable of infecting insects in dry conditions and of being mass produced, e.g., some spore-forming bacteria, particularly the *Bacillus thuringiensis* group that form crystals of toxic protein.

The toxin paralyses the host's gut and is probably responsible for the wide host range among the Lepidoptera. A few insects in some other orders are attacked at normal doses but no beneficial animals. I have tested seven storage moths to-date, *Anagasta kühniella* (Zeller), *C. cautella*, *Ephestia elutella* Hübner, *Hofmannophila pseudospretella* Staint., *Plodia interpunctella* Hübner, *Galleria mellonella* (L.) and *Achroia grisella* (F.). All are susceptible: 10^7 to 10^8 spores per gram of food cause 100 per cent mortality (10^7 spores = 50 p.p.m. of bacterial solids, costing about 7s. per ton of food treated). More economical methods of application are being sought.

The bacteria cannot attack vertebrates, in which huge doses of commercially produced bacteria are harmless. However, the bacteria could grow in some warm moist food preparations. Since the possibility that they may occasionally cause spoilage or produce unpleasant toxins cannot at present be ruled out, application to processed foods is best avoided at present. Dead preparations could possibly be employed. However, the one storage moth (*A. kühniella*) tested so far is not susceptible to the crystals alone. The crystal is a protoxin, which is broken by enzymes in the insect's midgut into two fractions, both lethal to susceptible Lepidoptera. Research may lead to the manufacture of these fractions and possibly others. Maybe they will be insect-specific, but with an increased host range.

Conclusions. Some pathogens will probably find specialised uses in Stored Products. Some may be limited by high costs. There are exciting openings for research.

CONTRIBUTED PAPERS

THE STATUS OF STORED-PRODUCT INSECT RESEARCH IN THE U.S. DEPARTMENT OF AGRICULTURE

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The object of this paper is to make a general assessment of the accomplishments, present status, and future outlook for research on stored-product insects in the U.S. Department of Agriculture. Overall contributions rather than detailed research data have been emphasized.

The level of research effort devoted to stored-product insects in the United States has been traditionally low in comparison with that on insects that attack crops during production. This has meant that it has been necessary for the studies on stored-product insects to be almost exclusively of an applied nature to meet the urgent need for control measures and information.

The development of practical control measures has been significant and varied. Numerous approaches to handling different problems can be grouped under the categories of fumigation, space and residual treatments for food and feed warehouses and for food processing plants, and procedures to control fabric insects. The trend toward preventive rather than control measures is illustrated by the development of protectants for bulk grain and peanuts in storage, and by significant progress in improving insect-resistant packaging.

During the research involved in developing the above measures, a considerable amount of effort has been devoted to obtaining residue data. These data have been made available to the Food and Drug Administration for consideration in relation to the establishment of tolerances under the Federal Food, Drug, and Cosmetic Act. Tolerance to cover the treatment of grains and other raw agricultural commodities are fairly adequate. These fall under the Miller Amendment, or Section 408 of the Act. Very few tolerances are established under Section 409, the Food Additives Amendment, to cover the use of measures to protect processed foods and prepared animal feeds. A large amount of research, with supplemental residue studies, is required to develop the data needed for establishing adequate tolerances. The additional chemical work that must now parallel the biological studies in developing control measures for stored-product insects makes the research much more complicated, time consuming, and costly than it was a few years ago.

It is increasingly evident that our applied research is hampered by a lack of basic information. In many lines of work we have reached the point of diminishing returns. Therefore we are diverting part of our effort to basic research even though a number of phases of applied research remain virtually untouched. A great deal of attention is needed on many lines of basic research in stored-product entomology. We are gratified that there seems to be an increasing recognition of the importance of this kind of research in this field in the U.S.A. It will require a vigorous, bold, and imaginative approach.

We must know more about the behaviour, physiology, and nutritional requirements of these insects to find better ways to combat them. Too much of our biological information is based on observations in the laboratory at ideal, constant, controlled conditions of temperature and humidity. We need to find out how they live and behave under the conditions of their natural environment. We must find new approaches to prevention and control. Parasites and predators, or the sterile male technique that gives such dramatic control of some insects are of no value to us. We cannot release thousands of insects in a warehouse or food plant to control the objectionable few already there. We must look further to preventive rather than control measures. We must preserve our food supply and at the same time avoid contamination by insects or hazardous pesticide residues. As the World population becomes greater and the food supply more critical, we cannot afford to place all our effort on producing crops and then permit insects to destroy them after harvest. There are better ways to be found for the safe, economical protection of our food, feed, fibre, and seed. They will be found through research. We must explore biological and physiological control, the use of electromagnetic energy of different kinds, and approaches that have not yet even been thought of. This is the challenge that faces the stored-product entomologist.

INFLUENCE DU MALE SUR LA FECONDITE D'*ORYZAEPHILUS SURINAMENSIS* L. (COLEOPTERE, CUCUJIDAE)

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La fécondité des femelles d'*Oryzaephilus surinamensis* placées dans des conditions identiques, présente une grande variabilité (1); ainsi Crombie (2, 3) a sélectionné des femelles de fécondité standard pour ses expériences sur la relation entre la fécondité et la densité.

Nous avons étudié la fécondité en fonction du nombre de mâles, de leur âge et de leur temps de présence dans des conditions identiques (t=25°C, RH=75% et obscurité constante); les individus utilisés étaient isolés avant la mue imaginale, dans des conditions semblables à celles de l'expérimentation. Le milieu d'alimentation et de ponte était constitué par Ig de pollen, dont la constance était préservée par maintien au froid (+6°C) avant utilisation, renouvelé tous les 14 jours (tableau I). Les oeufs ont été comptés et enlevés quotidiennement, et leur fertilité contrôlée.

Les relevés analysés portent sur les 60 premiers jours de la ponte des femelles ayant donné des descendants; toutes les femelles disparues en cours d'expérience ont été exclues des calculs. (tableau 2).

Dans tous les cas nous constatons une énorme variabilité liée au fait que dans toutes nos séries nous avons quelques individus dont la fécondité est anormalement basse. A titre d'exemple, voici les fécondités obtenues dans la série A: 1, 11, 47, 104, 115, 120, 137, 220.

Tableau 1

Expériences		*Femelles*		*Mâles*		
série	*nb. répétitions*	*nb.*	*âge au début expérience*	*nb.*	*âge au début expérience*	*durée présence*
A	n=8	1	1 jour	1	1-5 jours	10 jours
B	n=9	1	6-10 jours	1	6-10 jours	10 jours
C	n=9	1	6-10 jours	1	6-10 jours	permanent
D	n=7	1	10-15 jours	2	10-15 jours	5 jours
E	n=10	2	10-15 jours	1	10-15 jours	5 jours

Tableau 2

Série	n	ΣX	Σx^2	m	$s/\sqrt{n}$	m
A	8	755	36 688	94·375	25·599	115 34
B	9	557	32 361	61·889	21·200	111 13
C	9	537	24 146	59·667	18·312	102 17
D	7	1011	17 242	144·428	20·257	194 95
E	10	1271	111 787	127·100	35·244	210 47

Il n'y a aucune différence entre les moyennes des séries A, B et C. Par contre l'analyse de variance montre que la moyenne de la série D est significativement différente ($F = 115\cdot$ pour 1 et 31 D.L.) de celle de l'ensemble $A+B+C$; la différence est d'au moins 22 et d'au plus 125 oeufs.

Ceci montre que l'âge du mâle utilisé (1 à 10 jours) est sans influence sur la fécondité.

La série C, où le mâle est permanent, ne présentant aucune différence de moyenne, et la variabilité étant toujours aussi grande par suite de la présence de femelles à très faibles effectifs de ponte, ceci implique que la permanence du mâle n'apporte aucun bénéfice par rapport aux séries où il ne séjourne que 10 jours.

Dans la série E, où 2 femelles sont groupées dans chaque expérience, la fécondité moyenne est identique à celle des séries A, B et C, bien qu'elles n'aient disposé que d'un seul mâle pendant 5 jours; la variabilité est également très forte.

Par contre, l'augmentation considérable de la ponte moyenne enregistrée quand il y a 2 mâles (série D), bien que leur séjour commun ne soit que de 5 jours, montre que la différence est liée non pas à la nécessité d'une action prolongée des mâles, mais à la très grande variabilité de leur pouvoir inducteur de la fécondité.

Nous constatons par ailleurs que les femelles fécondes pondent plus de 90 jours après le retrait des mâles; certaines ont émis plus de 300 oeufs pendant cette longue période, sans que la fertilité ait diminué.

Dans les séries A et B, nous avons introduit un nouveau mâle auprès des femelles dont la fécondité était particulièrement faible et la ponte souvent terminée depuis longtemps (dans la série C, nous avons changé le mâle): après 90 jours d'expérimentation, nous avons déclenché une ponte régulière dans 80% des cas.

Ainsi la fécondité des femelles d'*Oryzaephilus surinamensis* ne dépend pas de la durée du temps de séjour du mâle, ni de son âge, mais de son pouvoir inducteur de la fécondité. Le rôle du mâle sur la multiplication de l'espèce est donc très différent de celui observé par Labeyrie chez *Acanthoscelides obtectus* Say, où pratiquement tous les mâles sont susceptibles d'induire la fécondité. Dans ces conditions, en présence de très faibles densités d'individus mâles, la multiplication de l'espèce n'est pas forcément assurée, étant donnée la carence d'un certain nombre d'entre eux.

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DIE WICHTIGSTEN VORRATSSCHÄDLINGE IN DER TÜRKEI UND IHRE BEKÄMPFUNG

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I. *Vorratsschutz in der Türkei: Einleitung.*

Der Schutz der Vorräte gegen Schädlinge ist in der Türkei ein ebenso wichtiges Problem, wie die Bekämfung landwirtschaftlicher Schädlinge überhaupt. Zahlreiche Arten von Vorratsschädlingen verursachen große Verluste. Mehrere türkische Entomologen studieren die Biologie, die Verbreitung, die Ökologie der wichtigsten Vorratsschädlinge, sowie die Methoden zu ihrer Bekämpfung. Jedem Pflanzenschutzinstitut ist ein Laboratorium für Vorratsschädlinge angeglidert. Ein Zentrallaboratorium für Vorratsschädlinge wurde vom Landwirtschaftsministerium vor etwa 2 Jahren in Ankara eingerichtet.

II. *Die wichtigsten Vorratsschädlinge*

(1) *An Getreide: Trogoderma granarium* Everts. Die Larven dieses Schädlings befallen insbesondere Weizen und Gersten. Der Schädling wurde im Jahre 1954 zum erstenmal in sudöstlichen Türkei gefunden. Andere wichtige Vorrätsschädlinge im Getreide sind *Sitophilus*

granarius L., *S. oryzae* L., *S. zeamais* Motsch., *Rhizopertha dominica* F., *Sitotroga cerealella* Ol. Als Sekundärschädlinge treten *Oryzaephilus surinamensis* L., *Cryptolestes* spp., *Tenebroides mauritanicus* L., *Tribolium* spp. häufig auf.

2. *An Getreide-Erzeugnissen: Anagasta kühniella* Zell., *Plodia interpunctella* Hbn., *Corcyra cephalonica* St., *Tribolium confusum* Duv., *T. castaneum* Herbst., *Tenebrio obscurus* L. und *molitor* L., *Acarus siro* L.

3. *An Hülsenfrüchten: Acanthoscelides obtectus* Say, *Bruchus pisorum* L., *B. rufimanus* Boh., *B. lentis* Fr., *B. ervi* Fr., *Callosobruchus maculatus* F., *C. chinensis* L.

4. *An Rohtabak, Zigarren und Zigaretten: Lasioderma serricorne* F., und *Ephestia elutella* Hbn.

5. *An Trockenfrüchten und Nüssen: Cadra cautella* Walk., *Ephestia figuliella* Greg., *E. elutella, E. calidella* Guen., *Myelois ceratoniae* Zell., *Plodia interpunctella, Anagasta kühniella, Paralipsa gularis* Zell., *Oryzaephilus surinamensis* L., *O. mercator* Fauv., *Carpoglyphus lactis* L., *Glyciphagus domesticus* Deg., *Rhizopertha dominica.*

III. *Verluste durch Vorratsschadlinge.*

Bei Getreide die jährlichen Verluste, die im ganzen Land entstehen, habe ich (1, 2) auf mindestens 10% geschätzt. Legt man 10% als Verlust zugrunde, dann bedeutet das, dass vährlich Getreide im Werte von rund 60,000,000 DM.—bei dem heutigen Kurs entspricht das ca. 200,000,000 Türkenpfund durch Schädlinge zerstört wird.

IV. *Vorbeugungs-und Bekämpfungsmethoden.*

1. *Schutz-(Einstaube-)mittel:* Getreide oder Hülsenfrüchte, die länger aufbewahrt werden sollen, werden mit einem anerkannten und vom Gesundheitsministerium zugelassenen Mittel behandelt. Pro Tonne Getreide oder Hülsenfrüchte werden ca. 500 g Malathion dust (2%) oder Pyrenone dust, Malathion Emulsion oder Pyrenone spray angewendet. Das geschieht in der Weise, daß man die Oberfläche der lagernden Produkte behandelt und anschließend gut mischt. Diese Verfahren sind im März 1963 vom türkischen Gesundheitsministerium zur Behandlung Getreide und von Hülsenfrüchten genehmigt worden. Praktisch angewendet werden sie noch nicht. Eine Verordnung wird zur Zeit vorbereitet.

2. *Begasungsverfahren.*

(*a*) Getreide: In den mit Kreislaufsystem ausgerüsteten Silozellen wurde früher Methylformat (Areginal) angewendet. Kleine Mengen Getreide werden mittels Methylbromid begast.

Mit Tabletten von Phostoxin wird Getreide sowohl in Silos, in Holz- und Betonlagern, in einfachen gasdichten Begasungskammern, in Schiffsladeräumen, in Bodengruben und selbst in offenen Lagern, die mit Zeltplanen (Tarpaulin) abgedeckt werden, begast. Auch in Silozellen und Begasungsanlagen werden die Tabletten mit gutem Erfolg verwendet.

Nach Angaben der Generaldirektion des türkischen Bodenamtes wurden zum Beispiel im Jahre 1963 rd. 80,000 ts Getreide mit Phostoxin-Tabletten begast. Phostoxin wird auch für die Begasung leerer Säcke und leerer Lager verwendet.

(*b*) Hülsenfrüchte: Seit einigen Jahren werden Hülsenfrüchte, die für den Export bestimmt sind, nämlich Linsen, Bohnen, Erbsen, Kichererbsen, Bohnenwinden und Wicken, in den Hafenstädten mit Methylbromid begast. Dazu benützt man stationäre und fahrbare entwesungskammern. Begasungen werden auch unter Zeltplanen ausgeführt. In den Jahren 1962 bis 1963 wurden rund 10,000 ts. Hülsenfrüchte begast.

(*c*) Trockenfrüchte: Feigen, Feigenpaste, Rosinen und Sultaninen werden teils von Genossenschaften, teils von privaten Firmen vor der Verpackung mittels Methylbromid oder einem Gemisch aus 75% Aethylendichlorid + 25% Tetrachlorkohlenstoff (Chorasol) in stationären Vakuumkammern, fahrbaren Kammern oder in einfachen gasdichten Kammern, teils auch in offenen Lagern, abgedeckt mittels Zeltplanen, begast.

Zur Begasung geschälter Haselnüsse, Walnüsse, Mandeln, Aprikosen-und Pfirsichkerne, ferner Pistazien wird teilweise Methylbromid verwendet.

(*d*) Auch Tabak, Cigaretten und Cigarren werden mit Methylbromid behandelt.

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DIFFERENCES BETWEEN IDENTICALLY REARED LABORATORY AND FIELD STOCKS OF THE FLOUR BEETLE *CATHARTUS QUADRICOLLIS* GUER.

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The developmental period and mortality of two stocks of the flour beetle *C. quadricollis* Guér. were compared under various conditions of temperature and humidity. The Dundee stock *ex* P.I.L. Slough, England, has been cultured under standard C.T. room conditions for some 12 years and then for a further 4 years in Dundee. The Nigerian stock had been in the U.K. less than a year. When the two stocks were compared by individual rearing in single tubes there were considerable differences in most parameters examined.

Fig. 1, however, illustrate the results of a group rearing technique. One hundred and fifty 1st instar larvae from each stock were collectively reared in groups of 25 per tube in each of 12 different conditions of temperature and humidity. To reduce disturbance factors due to observation techniques only the overall development periods and mortalities were recorded. Figs. 1a and c show for each a pattern of variation in which the quickest developmental period with the lowest mortality is around 27·5-28°C and 80-85% R.H. i.e. within the 20 day contour and the 20% mortality zone. Outwith these conditions mortality rates increase and developmental periods lengthen with negligible viability above 30°C or below 20°C and any humidity below 65% R.H. The similar patterns cannot, however, be superimposed and the Nigerian stock is very strongly favoured over a very much wider range of conditions than the Dundee laboratory stock. For both stocks it is also noted that the lowest mortality rates and quickest developmental periods only partially coincide to give the so-called "optimum" conditions which are approximately the same for each stock. However as environmental changes occur populations are selected to fresh "optima". The versatility to meet such changes is a prerequisite of "wild" stock and can be expected to reside in heterozygosity whereby alternative gene pathways may be redundant in a restricted environment but can there be expected to ensure the production of relatively uniform phenotypes. A more interesting statistic, and one possibly more useful in assessing populations for experimentation purposes, is therefore the coefficient of variation. Fig. 1b uses this statistic and the Nigerian stock is seen to show relatively uniform development over a vastly wider range of conditions than the Dundee laboratory stock which cannot be expected to be so heterozygous. Due to their usually numerically restricted origin and the standard method of subculturing, which relies on replenishment by the breeding of small samples in conditions of restricted artificial selection, laboratory stocks must tend to homozygosity. This genetic condition can be expected to fit them uniformly only to the narrow range of conditions to which they were selected and elsewhere to result in increasing phenotypic variability. Augmentation with new stock from the field will of course go some way to alleviate this condition. Such results are in accord with much of the work centering round phenotypic uniformity and genetic composition in fields concerned with the production of standard stocks for experimental purposes.

It is doubtful therefore whether it is good policy to base forecast and control measures, for use in the country of origin, on data issuing from the examination of partially inbred and strongly and artificially selected laboratory stocks.

It is suggested that maintenance of laboratory stocks should involve attention to genetic composition either by constant renewal from the field or continuous breeding in non-uniform environments.

Thanks are due to Dr. M. G. Morris, Statistical Department, Rothamsted, for assistance.

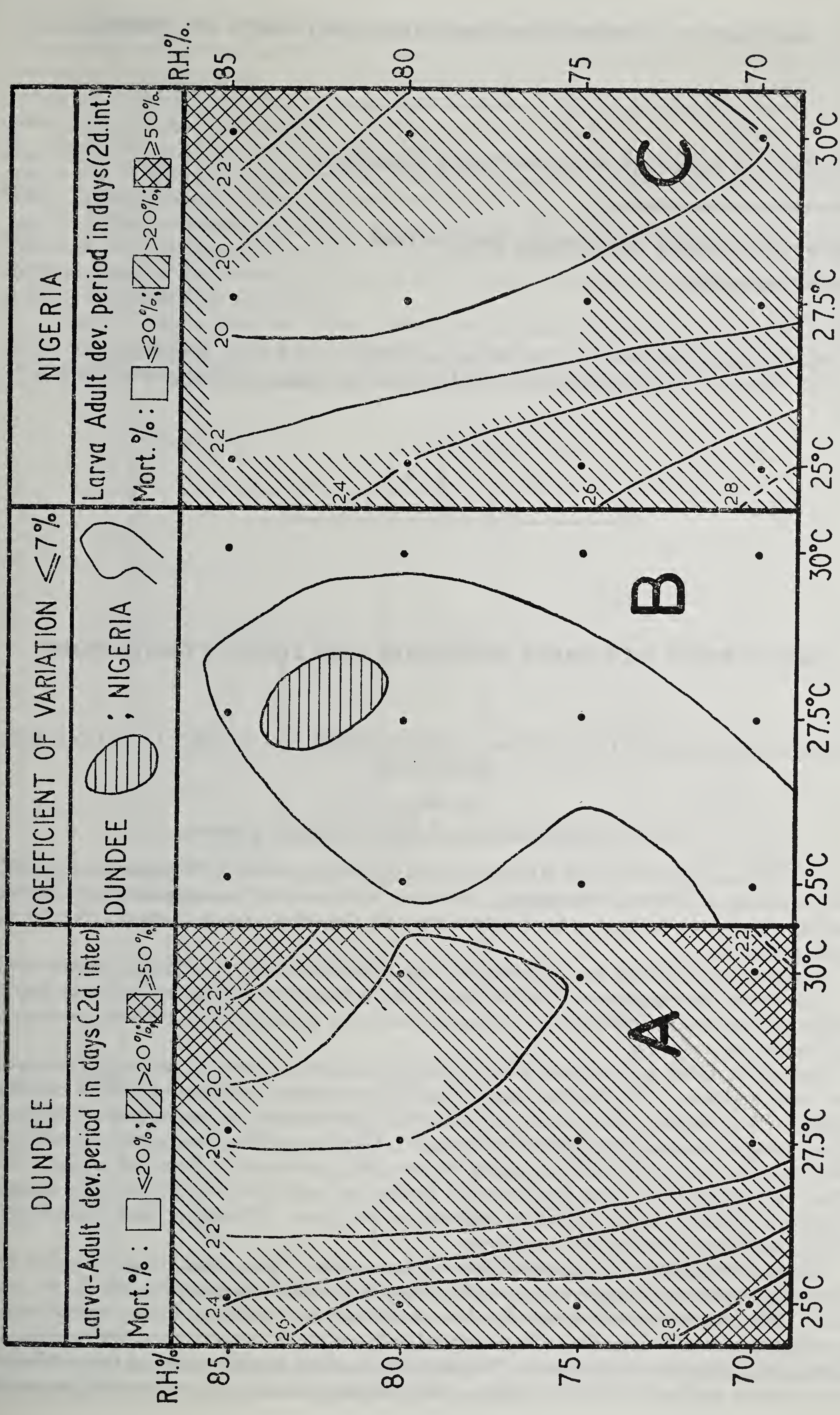

FIG. 1. a and c developmental periods and mortalities; b, coefficient of variation.

SECTION 10.—FOREST ENTOMOLOGY AND PESTS OF TIMBER

The following paper was read but the author did not wish it to be published here: Jones, T. (Kenya). The significance of tree-borers in the indigenous forests of East Africa.

INSECT PESTS OF FOREST NURSERIES AND YOUNG PLANTATIONS

BOURLETIELLA SIGNATA (NICOL.) (COLLEMBOLA)—A PEST OF CONIFER SEEDLINGS

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Probably most foresters think of Collembola as one link in the chain of organisms responsible for the breakdown of litter in forest soils. However, a few are well known pests of agricultural crops, e.g. *Sminthurus viridis* (L.) the Lucerne flea and *Bourletiella signata* (*hortensis*) (Nicol.) the garden springtail.

Search of the literature has revealed only one reference to injury to conifer nursery stock (5). However, the description of the damage to larch second year plants as similar to that of *Hylastes* (private communication) is quite unlike that to be described here and was consequent upon hoeing injury.

Bourletiella signata is a primary pest of various cruciferous crops (1), as well as potatoes, soya beans and peas. To this list may be added germinating seedlings of various conifers, especially *Pinus contorta*. Infestation coincides with germination and emergence of the seed, and both cotyledons and hypocotyl suffer damage. Conifer seeds are usually sown in the U.K. during March and April and, depending on weather, germinate in from 2-6 weeks. The earliest specimens of *B. signata* may be taken during the latter part of April and the nursery beds may be literally alive by mid-May and well on into June. Thereafter there seems to be a general and fairly sharp decline in numbers.

Affected seedlings tend to remain longer in the so-called "drum-stick" stage i.e. when the fully emerged seedling has the seed coat still adhering to it and retaining the tips of the cotyledons. The cotyledons have a curved or bent and untidy appearance. Under magnification the persistent drum-stick is seen to be associated with wilting of the cotyledon tips resulting in adhesion of the tips to the seed coat. Similarly the bending and distortion of the cotyledons can be seen to originate at feeding points. Such damaged seedlings show tiny lesions on the

hypcotyl as well. By the end of the first year the plants present a bushy appearance; little or no extension of the shoot will have been made but merely a proliferation of fattened distorted needles at cotyledon level. In fact, damaged plants were at first termed cases of "distorted contorta". Second year plants become multi-leadered, a feature which most nursery foresters recognise immediately as characteristic of one common type of cull.

Fig. 1 shows variations in rainfall and temperature at four nurseries. Two in Scotland and one in Yorkshire, are low in average rainfall, having in the region of 25 inches (635 m.) a year. The fourth, in S. Wales, has some 46 inches (1170 m). In the years 1959 and 1960 all four had May precipitation deficits, as can be seen from the diagram in which rainfall is expressed as a percentage of average. Their June records show no obvious pattern, however. In both years, in both months and at all four stations, temperatures show a significant and positive deviation from the average.

That *B. signata* likes the higher British spring temperatures seems apparent from its behaviour in the field. Far from seeking shade or shelter it is to be found in greatest numbers in the sunniest parts of the nursery and here, of course, the greatest damage results.

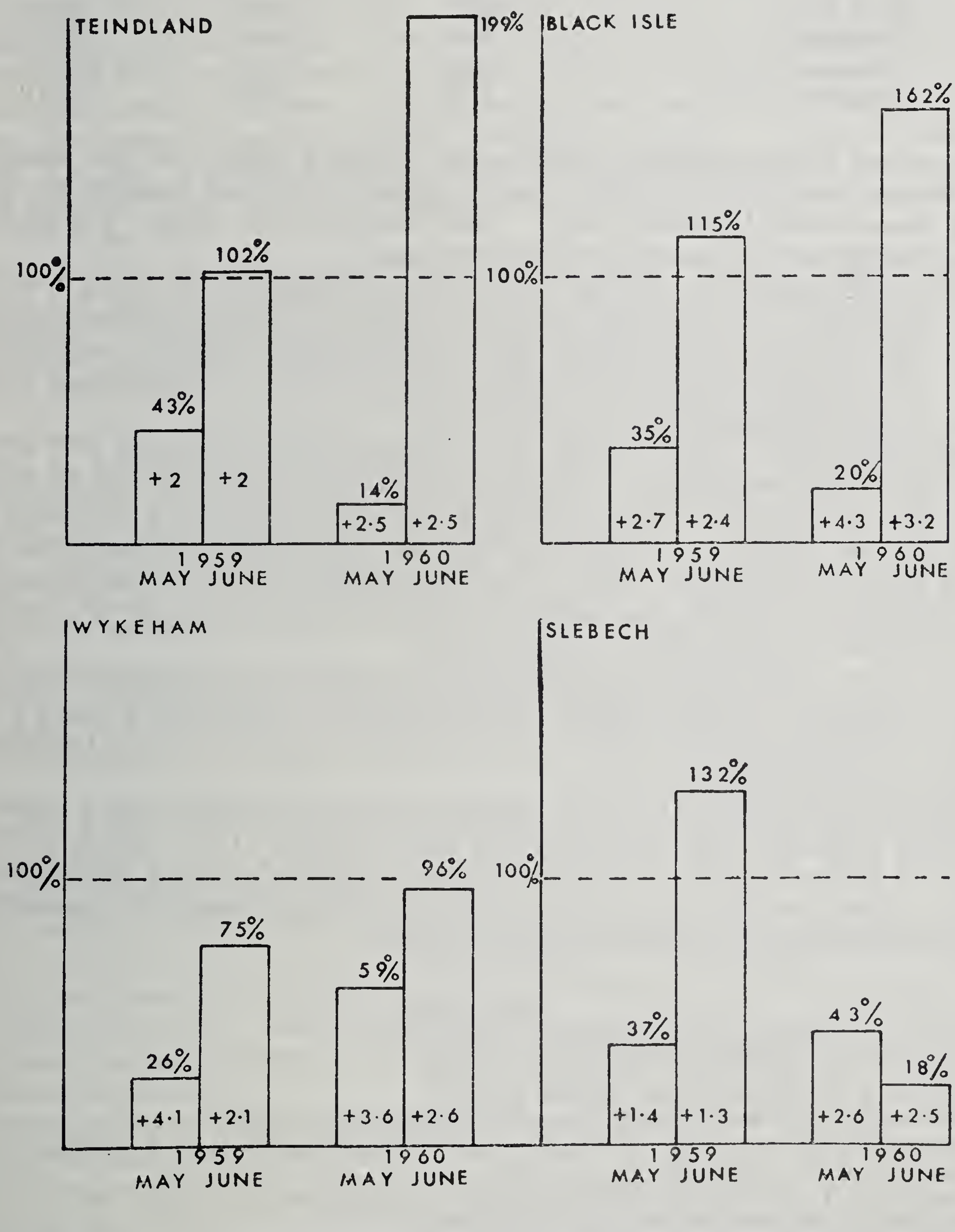

FIG. 1. Variations in rainfall and temperature at four nurseries: rainfall as percentage of average and temperature as deviations from the average.

DISCUSSION. It seems quite difficult to accept at first that any Collembolan does not require 100% R.H. Comparisons with *Sminthurus viridis*, which not only has been worked on thoroughly, but is also closely related to *Bourletiella*, show that in laboratory rearings (2, 6) survival is greatest at 100% R.H. Davies (2) showed that out of four species *S. viridis* was outstandingly more tolerant of low humidities than the others. Davidson (3) stated that "when the soil excreta surrounding the eggs are saturated, development is retarded and mortality may be high, particularly with temperatures below about 10°C. (50°F.) and above about 20°C. (68°F.)". Here is a positive indication that 100% R.H. may be definitely injurious to development, at least in one stage of the insect's life cycle. Davidson also stated that, although humidity is a critical factor in nymphal development, at 100% R.H. the nymphs may be seen on the wire gauze of breeding cages in contact with the outside air of lower humidity, and went on to define the temperature range over which he considered *Sminthurus* likely to be a pest as 52°F.-60°F.

TABLE 1

May temperatures in degrees F. for four nurseries

	Average	*1959*	*1960*
Black Isle	48·2	50·9	52·5
Teindland	50·8	52·3	53·3
Wykeham	48·8	52·3	53·5
Slebech	51·5	55·6	55·1

The average May temperatures and those for 1959 and 1960 for the four nurseries mentioned above are shown in the table. Thus the positive deviations recorded for these years placed *B. signata* within Davidson's range. June temperatures are some 3°F. above those for May and therefore put this month also within the range.

Observations consequent upon the outbreaks have shown that the insect is really quite common and damage on a small scale is very easy to find—not only to conifer seedlings but to a great number of weeds in the cotyledon stages, suggesting that *B. signata* is essentially phytophagous. Perhaps its low frequency or absence in species lists of subterranean Collembola (7, 8) may be regarded as giving some support to this.

FOREST IMPORTANCE. It is recorded in one nursery that an estimated 35% of the total yield of *Pinus contorta* seedlings were considered unusable and therefore had to be rejected. An interesting difference was noted in severity of attack upon seedlings of two sowing periods, April 4th-6th and 15th-22nd. These two lots reached their peak of germination on May 2nd and May 9th-13th respectively. 30% of the first sowing and 95% of the second were so severely damaged as to render them useless. This suggests that there may be a critical stage, the emerging period, when attack is most injurious.

Losses on the scale of those just mentioned are unusual; the multi-leadered cull, however, is not a rare phenomenon and a regular percentage loss due to substandard plants is accepted by foresters. What proportion of these rejected trees may be due to *B. signata* in a normal year has not yet been investigated.

Malathion 60 applied at 1½ pints 100 gallons/acre has consistently given a high degree of control, even when used in 2 or 3 consecutive years. Aldrin, D.D.T. and B.H.C. have all been tried as surface treatments—all at normal and therefore probably sub-lethal spraying rates (10). These materials produced an immediate but only temporary depression of the population and none gave an adequate degree of control.

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TERMITES IN FOREST PLANTATIONS

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1. *A Classification of Termite Damage to Trees.* Living trees are attacked by Isoptera in many parts of the world, but, although the groups causing the damage vary with the region, the nature of their approach falls into two main divisions:

(A) The colony is not only based on, but confined to, a single tree. The spread of attack to nearby trees can only take place when the colony is mature enough to produce winged reproductives, which fly off to found new colonies. Because of this limitation it is proposed to refer to these insects as "*Restricted Range Termites*". They belong to the two primitive families Kalotermitidae and Termopsidae. Important examples are *Neotermes tectonae*, which causes serious damage to teak in Indonesia, and *Porotermes adamsoni*, a pest of Eucalyptus in some parts of Australia. Their social organisation is of a relatively low order, and the colonies simply chew their way slowly through the wood.

(B) Those that have the ability to forage for some distance from their nests, so that a single colony is able to attack many trees. The term "*Free Range Termites*" indicates this lack of restriction in their movement. The four families involved are the Mastotermitidae, Hodotermitidae, Rhinotermitidae and Termitidae. *Mastotermes*, represented only in Australia, is not classed as a major forest pest. The Hodotermitidae, living typically by harvesting grass and other plant material, sometimes destroy seedlings in nurseries. Of the Rhinotermitidae *Coptotermes* is of great importance in Australia and Central America, where it hollows out the centre of standing, living trees. The large family Termitidae contains a number of genera which attack young trees.

2. *Damage Caused to Young Plantations.* The Restricted Range Termites, which are confined to older trees, will not be considered further, but the Free Range Termites damage young trees as well as mature. *Coptotermes* is principally an attacker of grown trees, but *C. amanii* in Kenya has been responsible for the death of *Araucaria cunninghamii* about three years old. The usual form of attack is for the termites to enter through the roots and hollow out the trunk, but examples have also been found which are atypical in that only the sapwood has been excavated.

By far the greatest damage to young trees is caused by members of the family Termitidae. In certain areas of Africa young plantations, especially of exotics and particularly of *Eucalyptus*, may be almost entirely destroyed. The degree of attack varies from ringbarking to the complete removal of the root. The principal offenders are in the genera *Pseudacanthotermes*, *Macrotermes*, *Odontotermes*, *Ancistrotermes*, *Microtermes* and *Microcerotermes*. The three last named may also excavate the stem interior. Some of these genera also cause damage in Asia, but are replaced in South America by *Syntermes*, which behaves in a similar way.

Attempts to define the conditions under which attack takes place have not been successful. There appear to be many factors involved, which are often difficult to record. The termites are not consistent in their reaction to such as have been recorded, and their activity in the same locality may vary from year to year. Attack is sometimes on the most luxuriant, sometimes on the poorest trees, and may be in the driest or the dampest corner of a plantation. Trees above 6,000 feet are not damaged, but below this altitude many areas are affected to some degree, particularly those with a long dry season.

3. *The Principles of Control.* Experience has shown that before control measures are applied it should be established that these are really necessary. Termites are often the scapegoat for bad silvicultural practice, and may be blamed when they are actually eating trees which are either dead or moribund. Care should be taken to ensure that tree species suitable for the area are used, and that in difficult terrain they have good roots, preferably having been grown in individual containers.

Control may be attempted in two ways—by the destruction of the termite nests—or by preventing the insects from approaching the trees.

To destroy the nests it is necessary to be able to locate them, and this is only possible in practice with those species which build mounds or make vent holes in the ground. The ease with which a colony may be killed depends on the nest structure, as some systems are much more resistant to penetration by insecticides than others. Toxic smoke is favoured in South

Africa, but in other parts of the continent applications of fluid to the nest interior have been found the most satisfactory method.

The majority of pest termites build subterranean nests which cannot be found, so that protection of the trees is necessary. A broadcast treatment of insecticide is sometimes used, but this method is not to be recommended. The full results of the general destruction of soil fauna and the long-term effects on soil structure and chemistry are not known, and as spot treatments are satisfactory broadcast methods should be avoided. For the same reason experiments on the use of repellents instead of insecticides are to be encouraged. Several satisfactory methods of protecting individual trees are now known, the choice depending on local requirements and facilities. As attack may come from any direction in the soil, it is essential to ensure that the protective barrier is complete. Treatment of the young plants in the nursery is without doubt the most economical approach. Insecticide can be either mixed in the potting soil as dust, a method pioneered by Sands in Nigeria; or watered on to the young stock in the form of diluted emulsifiable concentrate or wettable powder, a system which has been proved very effective in Northern Rhodesia. Nursery application is only suitable when the trees can be planted out at the same level. If deep planting is necessary, resulting in a length of stem being buried, then field treatment is essential. Complete protection can be obtained by mixing insecticide in the hole when planting out. This can be applied in dust or liquid form. The former is rather more expensive, both in labour and material, but must be used when diluent water is not conveniently available.

INVESTIGATIONS ON PLANTATION WEEVILS IN CANADA

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The number of seedlings distributed by government nurseries for planting is a useful guide to the scope of tree planting in Canada. The annual distribution of seedlings by provincial nurseries has been steadily increasing since early in the present century and by 1960 approached 74 million. The Canada Department of Agriculture also distributes about six million seedlings annually from two nurseries in Saskatchewan for the establishment of shelterbelts. Plantings from all government and private sources in Canada perhaps exceed 100 million annually. Coniferous species predominate in plantations used for the production of lumber, pulp, and Christmas trees. These plantations in some areas are accompanied by severe weevil attack, with the most destructive species falling into the genera *Hylobius*, *Pissodes*, and *Steremnius*.

Ecological studies on weevils in Canada have tended to be fragmentary and discontinous, one of the reasons being confusion in the recognition of allied species. Some of this confusion is being remedied by continuing studies on the cytosystematics of weevils by my colleague, S. G. Smith. His early comparison of the karyotypes in *Hylobius* species helped to establish the separation of *H. pinicola* Couper from *H. warreni* Wood. His present studies are basic to an understanding of evolutionary trends in speciation within the genus *Pissodes*. Smith's examination of the karyotypes of 15 species of *Pissodes* showed that they fall into five groups between which reproductive isolation was expected, and this expectation is being confirmed by compatibility tests. One group of particular interest contains three injurious species that are practically inseparable by cytological and conventional methods. These species are *P. strobi* Peck, *P. engelmanni* Hopkins, and *P. sitchensis* Hopkins, which commonly attack white pine in eastern Canada, engelmann spruce in the Rocky Mountains, and sitka spruce near the Pacific Coast, respectively. Thus the most significant differences between these species are associated with preferred hosts and geographic distribution.

Probably the most destructive weevil in Canada is *P. strobi*. From studies by my colleague C. R. Sullivan it appears that susceptibility of pines to attack by *P. strobi* relates to the physical characteristics of the leaders and that the microenvironment of the leader may determine the intensity of attack. The importance of the physical factors is being tested by J. C. Heimburger

(Dept. of Lands and Forests) who, by grafting techniques, is showing that stock selected for resistance is indeed relatively resistant to weevil attack, although there is variability within and between clones. The role of the microenvironment is being investigated by W. M. Stiell and A. B. Berry (Petawawa Forest Experiment Station), but their work has not progressed to the point of drawing definite conclusions.

The popularity of red pine as planting stock has been attended by high mortality of young trees, especially in central Ontario. An undetermined disease organism and *P. approximatus* Hopk. are contributing factors, but J. L. Martin has shown that the weevil alone is capable of killing young pines when they are planted near older red pine stands where sanitary measures of slash removal are not practised.

Other major weevil pests of coniferous plantations in Canada are *P. terminalis* Hopping, *P. affinis* Randall, *H. pales* Herbst, *H. radicis* Buchanan, and *Steremnius carinatus* Boh. *S. carinatus* was only recently reported by R. R. Lejeune (Forest Entomology and Pathology Laboratory, Victoria, B.C.) as a serious pest of Douglas fir and other conifers in western British Columbia.

RECENT ADVANCES IN THE STUDY OF *HYLOBIUS* SPECIES INFESTING THE ROOTS AND ROOT COLLAR OF PINE IN CENTRAL NORTH AMERICAN PLANTATIONS

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Three weevils in the genus *Hylobius* constitute a major threat to the successful culture of pine plantations in the western Great Lakes region of central North America.

Hylobius radicis larvae infest *Pinus banksiana* Lamb., *P. resinosa* Ait., *P. sylvestris* L., and several North American and European species used for reforestation. Persistent infestations are reflected in reduced radial and terminal increment, an almost complete cessation of growth of the root collar, an enlargement of the stem above the root collar, and a gradual decline in vigor. The tree may survive for several years, then die or be windthrown. Highest populations occur in 4 to 20 year old plantations and windbreaks established on light, sandy soils, particularly where spacing has exceeded 6 × 6 feet or survival has been poor.

Hylobius rhizophagus larvae infest the roots of *Pinus banksiana* and *P. resinosa* and is known only in north central Wisconsin. Attack is primarily on pole size, stagnating, 15 to 30 year planted forests. In areas of high weevil populations, naturally occurring 1 to 5 feet reproduction frequently is infested. Early symptoms include isolated groups of trees showing a rapid decline in vigor with dying branches scattered throughout the crown. Needles on these affected branches generally are shorter than normal. As the infestation increases in intensity, groups of trees die and adjacent trees show the early symptoms. Ultimately, the entire plantation succumbs. Reproduction invading the recently killed plantation also may be infested and die in a single season; the needles turn brown without a reduction in length.

Similar symptoms were observed on 8 year old Christmas tree plantings of *P. sylvestris* and *P. resinosa* in west central Wisconsin in 1963.

Hylobius pales larvae infest the stumps and roots of recently cut natural and planted pitch and soft pines throughout eastern North America. The adults feed voraciously on the bark of young reproduction and cause mortality of small trees and branch mortality on larger saplings. In 1962, a plantation of *P. sylvestris* was examined where a few dead branches were present on the crowns of many trees. Harvest of Christmas trees had begun two years earlier and the bottom whorl of branches on the stump often was left to promote a second merchantable tree. All stumps were left intact. The stumps and roots of cut trees, including those on which one bottom whorl of branches remained, were infested by *H. pales*. The roots of trees on which dead branches occurred were adjacent to the fresh stumps and also showed evidence of root invasion. The adult feeding on the branches was insufficient to cause the branch mortality.

LEPIDOPTERES ESPAGNOLES NUISIBLES AUX PEPINIERES ET AUX JEUNES PLANTATIONS

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Dans ce travail, on receuille les données sur les dommages causés par les lépidoptères dans les pépinières et les jeunes plantations, qui ont été observées en Espagne par les techniciens du Servicio de Plagas Forestales, depuis la fondation de ce centre en 1952.

Les espèces botaniques auquelles se concentrent les observations sont les peupliers, les pins, et dans un seul cas, l'eucalyptus.

Quant aux peupliers (*Populus*), on a enregistré comme défoliateurs: *Dicranura vinula* L., 1758; *Thaumetopoea pityocampa* Schiff., 1775; *Apatele megacephala* Schiff., 1775; *Leucoma salicis* L., 1785; *Smerinthus ocellata* L., 1785. Les plus nuisibles sont: *D. vinula* et *L. salicis*. Comme perforateurs des branches on a les suivantes: *Aegeria apiformis* Cl., 1779; *Paranthrene tabaniformis* Rott., 1775, et *Gypsonoma aceriana* Dup., 1843. Grâce aux investigations faites par le Servicio de Plagas Forestales, on a découvert que *P. tabaniformis* fût capable de profiter du développement de la populiculture espagnole pendant les dernières années, en proliférant dans tous les endroits. Jusqu'à 1952 on ne l'avait vu que dans 7 provinces espagnoles, et depuis cette date, le Servicio de Plagas Forestales l'a trouvé dans 24 de plus. Au contraire, *Aegeria apiformis* qui jusqu'à cette année avait été identifié dans 8 provinces, n'a pu être trouvé que dans 2 autres, ce qui paraît démontrer qu'il n'a pas pu s'étendre autant que la *tabaniformis*. Bien que tous les auteurs espagnols, à partir du travail de Cadahía en 1958 ("Graellsia", t. XVI; 69-74) nous parlent de *synagriformis* Rbr. somme une sous-espèce ibérique de *tabaniformis*, j'ai pu constater que la sous-espèce tiponominale habite aussi dans le versant cantabrique selon des exemplaires de Villapresente, dans la province de Santander, et je soupçonne que l'on pourra constater l'existence ici de *tabaniformis rhingiaeformis* Hb., qui avait été déjà nommée par Zerny d' Albarracín, à Teruel, en 1927, ("Eos", t. III: 445). Quant à *Gypsonoma aceriana* Dup., 1843, elle cause, selon Dafauce, des dommages plus graves dans les pépinières et dans les jeunes plantations, puisque les jeunes peupliers sont déformés dès qu'ils perdent leur guide terminale. Le seul mineur identifié jusqu'à présent dans les pépinières espagnoles, est *Lithocolletis populifoliella* Tr., 1832, que j'ai déterminé de Moralzarzal, Madrid.

L'Ingénieur Cadahía a trouvé la commune et polifage *Plusia gamma* L., 1758 en mangeant les feuilles de l'eucalyptus dans une pépinière de la province de Huelva.

Quant aux pins, la défoliatrice *Thaumetopoea pityocampa* Schiff., 1775 a une plus grande importance sur les jeunes plantes que sur les arbres développés, selon Romanyk en 1963 ("Bol. Serv. Plagas Forestales" t. VI: 21), puisque ces attaques répétés tuent les premières et jamais les secondes. Sur les guides terminales et les branches latérales, la *Petrova resinella* L., 1756 a moins d'importance que la *Rhyacionia buoliana* Schiff., 1775; et celle-ci, comme l'a confirmé Arana Santoyo, passe des forêts aux pépinières que sont proches. Alors, dans cette année de 1964, les spécialistes du Servicio de Plagas Forestales ont découvert que *Rhyacionia duplana* Schiff., 1775 est dans les pépinières espagnoles beaucoup plus nuisible que *Rh. buoliana*, dans lesquelles, on doit dire en passant, elle est très répandue. En 1960 ("Bol. Serv. Plagas Forestales", t. III: 128) j'ai traité déjà les dommages causés par *Dioryctria nivalensis* Rbl., 1892, dans les jeunes replantations de *Pinus insignis*, à l'île de Ténériffe. Finalement, Rupérez m'a informé de ses observations sur les dommages de *Spodoptera littoralis* B., 1833, sur les racines de *Pinus halepensis*, dans une pépinière de Sierra Espuña, Murcie.

THE OVERWINTERING OF THE LARCH THRIPS *TAENIOTHRIPS LARICIVORUS* KRATOCHVÍL AND FARSKÝ

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These investigations took place in the reforestation area "Copera" near Bellinzona in the south of Switzerland. This area covers about 100 acres and lies between 1,500 and 2,500 feet above sea level on the northern slope in the chestnut zone. In addition to the various broad-leaf tree species there are Douglas firs, Weymouth pines, larches, spruces, Scots pines, silver firs and Himalaya cedars. With the exception of the larches, which are now 30 feet tall, these conifers reach heights of up to 11 feet.

450 trees of the above species were examined in the autumn and winter for larch thrips and were found to be colonized by more than 4,600 female thrips. In addition to the known winter host (spruce), Douglas fir, Weymouth pine and Himalaya cedar were recorded as hosts for the first time,—the cedar much less frequently than the others (see below).

On the spruce and the Douglas fir most larch thrips spend the winter under the protection of the previous year's bud scales. Out of 987 females on 40 spruces only 13 (1·3%) were found in axils of terminal needle clusters or under loose scales of the current year's buds. Under the latter on Douglas fir also, only 4·2% of the adults were found, based on 932 thrips on 40 trees. On Weymouth pine practically all the females are to be found under the current year's bud scales of the terminal needle clusters. On other needle clusters on 20 trees only 2 out of 229 thrips (0·9%) overwintered under the bud scales. On the cedar only small hiding places between the needle base and the shoot axis are available.

Vertical distribution of the larch thrips shows that on spruce and Douglas fir the majority spend the winter on the shoots of the second uppermost whorl; above and below the number of adults diminishes. On Weymouth pine most of the thrips overwinter on the branches of the top two whorls and in contrast to spruce and Douglas fir the population density of these two levels is about equal.

The light requirements of the larch thrips is the main factor in the choice of trees for overwintering. Spruces, Douglas firs or Weymouth pines which stand alone in the middle of the larches are seldom chosen, in contrast to trees on the border. It also appears that the prevalent wind direction, at least in slope areas, plays a role. As an example I refer to the results taken from two comparable spruce plantings, one lying down-wind from the larch field, the other transverse to the wind direction. In the former, 240 thrips were found on the branches of the two top whorls of 10 trees and in the other only 75. (Population density per shoot examined: second uppermost whorl 6·8: 1·3 and the top whorl 0·5: 0·1).

The distance from the nearest larches is also of importance in the selection of winter quarters, particularly in connection with the prevalent wind direction. A distance of 120 feet down-wind has scarcely any effect on the colonization density; on the other hand the distance transverse to the wind direction plays a role. As an example: on each of 10 spruces directly adjacent to larches were 406 thrips, while 120 feet away down-wind 372 were found. A similar sampling from each of ten Weymouth pines over about the same distance, but transverse to the wind direction, indicated 143 compared to only 3 larch thrips.

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INSECT PESTS OF FOREST NURSERIES AND YOUNG PLANTATIONS IN NEW ZEALAND

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FOREST NURSERIES. In forest nurseries in New Zealand far greater losses are caused by fungi than by insects.

The important soil-inhabiting insects are the Melolonthinae, mainly *Odontria* and *Costelytra* spp., and the weevils *Graphognathus leucoloma* Boh. and *Xerostygnus binodulus* Broun. Of minor importance are the weevils *Otiorrhynchus sulcatus* Fabr., *Phlyctinus callosus* Boh., and *Asynonychus cervinus* Boh., the noctuids *Agrotis ypsilon* (Rott.), *Euxoa admirationis* (Guen.), and *Melanchra* spp., and the hepialids *Oxycanus* spp. All these insects feed on the roots and root collars of seedlings, the greatest mortality being usually observed in spring. Only a few larvae present in each square foot can cause considerable damage, and therefore complete eradication of soil-inhabiting insects is aimed at.

In the nurseries of the New Zealand Forest Service, prior to 1956, DDT at a rate of 5 pounds per acre per annum was used for the control of Melolonthinae. In 1956, this and even double this rate failed for some unexplained reason to control these insects in the nursery of the Forest Research Institute. At present the recommended insecticide is dieldrin applied at the minimum rate of two pounds per acre per annum. Another application can be made if insects are still found within the same year. No side effects on plants have been observed after application of dieldrin, and so far no insect resistance to it has been noticed. More investigations are needed to determine the minimum amount of insecticide necessary and the best time of application.

The Melolonthinae, which are a major pest of pastures in this country, have given little trouble in recent years in forest nurseries after application of dieldrin at the recommended rate.

Graphognathus leucoloma, the white-fringe weevil, is established only in restricted localities in the North Island. It may develop into a serious pest and has already caused severe damage to *Pinus radiata* seedlings in nurseries around Auckland. The infestation originated from surrounding pastures and areas of bush lupins (*Lupinus arboreus*). Only up to three or four larvae per square foot were present in seed beds during the period of heavy mortality. Adults are all females incapable of flight. A higher rate than two pounds of dieldrin is necessary for control.

Xerostygnus binodulus, a native weevil, occurs in several nurseries. Recently it has caused severe mortality to larch and Douglas fir seedlings in Kaingaroa Forest. The larch seed beds, which showed a mortality of 60%, had not received any insecticide treatment. The Douglas fir seed beds, where mortality was estimated at 400,000 seedlings were treated with one pound of dieldrin per acre at sowing, but heavy rain soon fell afterwards. It appeared that this insect is associated with sorrel (*Rumex acetosella*), which was present in all the infested seed beds. Trials with various insecticides will be undertaken.

Damage caused by *Hylastes ater* (Payk.) feeding on the root collar of pine seedlings has been reported from nurseries where surrounding pines have been felled.

Lepidoptera. The main lepidopterous defoliators attacking exotic conifers in nurseries are the tortricids (*Epiphyas postvittana* (Walk.), *Tortrix excessana* (Walk.), *T. distincta* (Salmon) and *Ctenopseustis obliquana* (Walk.), while these and two eucosmids (*Spilonota macropetana* Meyr. and another undetermined *Spilonota* species) attack eucalypts. Of minor importance to the exotic conifers are the geometrids *Selidosema suavis* (Butl.), *S. fenerata* (Feld.), *S. leucelaea* (Meyr.), *Declana floccosa* Walk., *D. leptomera* (Walk.), the noctuids *Pseudaletia separata* (Walk.), *Heliothis armigera* Hübn., and the psychid *Oeceticus omnivorus* (Dbld.). The chrysomelid *Eucolaspis brunneus* Fabr. is occasionally troublesome.

Sap sucking insects are of minor importance, as they are easily controlled by spraying. The adelgid *Pineus boerneri* Annand is found on pines, the aphids *Elatobium abietinum* (Walk.) on spruces, and *Neochmosis juniperi* (Geer) on *Cupressus*, *Thuja*, and *Juniperus*.

The native longhorn *Oemona hirta* (Fabr.), which bores in the stems of hardwood species, is difficult to control.

YOUNG PLANTATIONS (up to ten years old). The most troublesome insect in *Pinus radiata* regeneration is the European scolytid *Hylastes ater* (Payk.). Emerging adults from slash and stumps ringbark seedlings at ground level. Mortality of over 50% has been recorded, but is only significant in poorly stocked areas. Planted stock of other pines and of Douglas fir is often severely attacked. Also damaging in regeneration are the noctuids *Melanchra* spp., *Agrotis ypsilon* (Rott.), *Ariathisa comma* (Walk.), subterranean grass caterpillars (*Oxycanus* spp.) and Melolonthinae. The thrips *Heliothrips haemorrhoidalis* Bouché occasionally cause death of regeneration growing under a canopy.

The Tortricidae mentioned under "Forest Nurseries" feed on the foliage of exotic conifers. Damage is usually not severe, even when large numbers are present, but attack on terminal buds and developing shoots invariably results in malformation.

Nine species of Geometridae (those mentioned above and *Selidosema productata* (Walk.) *Declana hermione* Hudson, *D. junctilinea* Walk., and *Hybernia indocilis* (Walk.)) attack exotic conifers. Damage is usually slight as larvae do not occur in large numbers, but during epidemics of *Selidosema suavis* in Canterbury in 1951-52 and 1960-62 young regeneration along roadsides was stripped.

A scorched appearance of young pines in summer is caused by feeding of *Eucolaspis brunneus*. The katydid *Caedicia simplex* Walk. causes minor defoliation, and *Pineus boerneri* attacks pines, but attack at present is seldom heavy.

Larvae of *Navomorpha lineata* Fabr. ringbark twigs and branches of Douglas fir, causing wind breakage. Main stems are occasionally attacked.

Sirex noctilio (Fabr.) and its associated fungus is responsible for mortality of pines after the onset of competition.

On *Eucalyptus* species the most important defoliator is the chrysomelid *Paropsis charybdis* Stål, followed by the weevil *Gonipterus scutellatus* Gyll., *Spilonota* spp. (Eucosmidae), and *Antheraea eucalypti* Sc. (Saturnidae). Occasionally severe attack by the scale *Eriococcus coriaceus* Mask. occurs on young twigs and branches. *Hepialus virescens* (Dlbd.) has been found to bore in branches. Of minor importance on the eucalypts are the aleyrodid *Aleuroclava eucalypti* Dumb., the psyllid *Ctenarytaina eucalypti* (Mask.), the gall forming eulophid *Rhicnopeltella eucalypti* (Gahan) and the defoliators *Eucolaspis brunneus*, *Tortrix excessana*, *Ctenopseustis obliquana*, *Declana leptomera*, *D. floccosa*, and *Selidosema suavis*.

TROPICAL FOREST ENTOMOLOGY

INFESTATION OF *PINUS CARIBAEA* BY THE TERMITE *COPTOTERMES NIGER* SNYDER

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There are many records of termite attack on mature trees, but close study of the problem has been made in only a few cases. Attack on sound heartwood may take place through dead rotting wood on the tree or through the living bark and sapwood. Both methods of attack are used by *Coptotermes acinaciformis* and *C. brunneus* in Australia (1). In these and other well studied examples the attack is primary and not dependent on earlier fungus attack, apart from

the requirement for entry into the tree in some cases. Termite infestation of the heartwood of the highly resinous British Honduras pitch pine has been regarded as a serious problem, the frequency of infested trees being found to exceed 80% in some areas. The writer studied this problem, mainly in the coastal pine savannah and woodland of the Stann Creek district, following the identification of the termite by Harris (2).

Coptotermes niger is found in all the pine dominant areas of the country, which are well described by Lamb (3). It forms large colonies, nesting in the soil, litter or piped trees, and shows some feeding preference for the slightly rotten pine sapwood of litter. The investigation has shown that a brown rot is present in all cases of heartwood infestation of *P. caribaea.* The termites are confined to the rot infected heartwood and appear unable to penetrate the sound wood at all, except by the trivial enlargement of shakes. Often a tree is found abandoned by the termites after the rotten wood is exhausted. On the other hand the rot often occurs in the absence of termites. Rot infection takes place mainly through fire scars, sometimes through upper roots or damaged branches. It is never initiated by termite attack as the termite cannot penetrate the living tissue of a healthy tree or the resinous wood of wounds and so can only follow the fungus into the tree. The fungus was cultured by Mr. J. G. Savory of the Forest Products Research Laboratory and identified as *Lentinus pallidus.*

A series of laboratory tests were carried out involving comparisons of life length amongst groups of worker termites exposed to various woods in glass plates, with starvation controls. These are to some extent summarised by one experiment, the main results of which are given below:

Treatment	*Mean 50% mortality of workers (Days)*
Rotten heartwood	32·6
Sound heartwood less all resin	26·2
Sound heartwood less turpentine	20·0
Sound heartwood untreated	10·4
Starvation	9·4

In this and other experiments no significant difference was found between untreated heartwood and starvation, but life length in rotten heartwood was always highly significantly and grossly greater. Scarcely any feeding or penetration took place in sound untreated heartwood, but in the above test repellence to penetration and, as the figures indicate, the greater part of repellence to feeding were removed by removal of the turpentine fractions; some repellence to feeding appeared to lie in the rosin content of the wood.

This then is a case of frequent and heavy heartwood infestation of a tree by a termite which cannot in fact attack the wood at all, being wholly secondary to a rot fungus. Such a situation may not be common in tree infestations, but clearly one must check against it whenever rot is present in order to determine whether the termite or the fungus is the true attacker.

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INSECT DAMAGE ON EXOTIC CONIFERS

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In East Africa extensive plantations of exotic Pines and Cypresses have been established during the last two decades. As these areas expand and mature there is an increasing danger from defoliator outbreaks, particularly of indigenous species, and there have already been some minor outbreaks in Uganda, Kenya and Malawi. The problems associated with such outbreaks in tropical areas, although basically similar to those associated with outbreaks in the temperate zones, have some important differences, as has become apparent from the study of outbreaks in Uganda.

The problems fall into three groups, namely climatic, economic, and those associated with host selection.

The effect of climate is most important, particularly the prevailing high temperatures and the absence of any season that is particularly unfavourable to either insect or tree development. As a result defoliating insects can achieve 3 or more generations in a year and outbreaks can build-up extremely rapidly; this produces problems of both assessment and control. A permanently favourable climate also tends to produce a population which, at any one time, contains a species in all its stages of development. This complicates population assessments and may also adversely affect chemical control; however, biological control will probably be favoured by this same lack of periodicity.

The effects of climate may also be favourable to the survival of the host tree: its recovery following partial defoliation will be hastened, thus reducing the period during which its vigour is reduced and secondary attack is more likely. The rapid height growth typical of these exotics may also be advantageous, taking the growing point above the height range of some insects within one or two years.

Economic problems arise from the long-term nature of forestry and the comparative poverty of the developing nations. Both factors make it imperative that any control measures applied to these defoliator outbreaks are as cheap and as permanent as possible. As a result, chemical control will need to be restricted to a minimum and there will be considerable scope for the use of biological control. The prospects for the successful use of biological control are good for the indigenous defoliators, but the appearance of an introduced defoliator could cause serious problems.

Problems of host selection arise from the lack of indigenous conifers in East Africa. These are restricted to *Juniperus* and a few *Podocarpus* species and there are no indigenous Pines or Cypresses, the principal exotics being introduced. As a result all the defoliators appearing on these exotics have previously fed on broad-leaved trees, herbs and grasses: this sharp change of host produces a number of problems, one of which is the lack of prior information as to which species are likely to develop into pests of the coniferous plantations.

The problems arising from the establishment of extensive plantations of exotic conifers are likely to increase in both diversity and intensity. With forest entomology still in its infancy in East Africa they will necessitate much basic research, particularly in the fields of biological control and bioclimatology, and a flexible and broad outlook on such research will be essential.

THE INCIDENCE AND CONTROL OF INDIGENOUS INSECT PESTS OF KENYA FOREST PLANTATIONS, WITH PARTICULAR REFERENCE TO WOOD BORERS IN EXOTIC CROPS

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Though there are more than 100,000 acres of plantations in Kenya, some 70,000 of which are exotic softwoods (Pines and Cypresses) and about 15,000 of exotic hardwoods (*Eucalyptus* spp.), the only major indigenous insect pests which have so far been found are Cerambycid borers in living trees. Of these *Oemida gahani* Dist. is of the greatest importance though its major damage is confined to *Cupressus* spp., which form rather less than half of the total softwood plantation area.

Other pests, such as defoliators and bark beetles have occurred in sporadic outbreaks affecting only small areas, the maximum of which was 27 acres of *Pinus radiata**. The commonest of these minor pests are as follows:—

Defoliators

Of the exotic plantation species, *Pinus radiata* appears so far to be the most susceptible to this type of damage.

The bagworm *Semimanatha aethiops* Hamps. (Psychidae) is one of the only two defoliators which have caused appreciable damage. In 1950 some 27 acres of a 10 year old *Pinus radiata* plantation was completely defoliated. The attack did not spread however to neighbouring plantations, and died out during the following year, though no sign of parasites or disease was found to account for this. Some ten years later another outbreak occurred during a period of drought which completely defoliated about 5 acres in a 100 acre block. Spraying was about to be used to control it, when a period of floods intervened and the outbreak died out. No controlling agent was discovered in this case either.

Other defoliators attacking *Pinus radiata* primarily are *Orgyia mixta* Snell. (Lymantriidae) and *Gonometa podocarpi* Aur. (Lasiocampidae). They are both kept under control by indigenous parasites including Tachinidae—*Tachina fallax* Meig, and *Sturmia gilvoides* Curr., Braconidae—*Apanteles africana* Cam. and Ichneumonidae—*Pimple mahalensis* Grib. No appreciable damage by these insects has so far been recorded.

Eucalyptus spp. are frequently attacked by Saturniid larvae such as the species *Nudaurelia gueinzii* Karsch. but the only important damage to plantations by this family was to the indigenous *Juniperus procera* by *Nudaurelia rhodina* Roths. when some 21 acres were affected. This outbreak died out from unknown causes, but a smaller outbreak a few years later in a distant forest area affecting some 2 acres was controlled by an unknown disease, probably bacterial or virus.

Bark Beetles

Only one species—*Phloeosinus schumensis* Egg. has caused any damage and this only to *Cupressus* spp. affected by drought or disease. The beetles tend to enter near the axils of the branches of such trees and often kill them by their girdling effect, which contributes to the final death of the tree. Slight damage has occasionally been found to the twigs of healthy trees which may be killed in the same manner. This insect commonly attacks freshly felled logs and may thus be a potential danger to *Cupressus* plantations when a population builds up in unsaleable thinnings.

Borers in living trees

It is significant that *Cupressus* spp. are the only exotic plantation trees to be affected by these insects and of the indigenous plantation species only *Juniperus procera* (E. A. Cedar), which is also a member of the botanical family Cupressaceae. These two genera comprise a total plantation area of more than 40,000 acres, the majority of which are situated in the areas of highest incidence of the pest between altitudes of 5,000 and 9,000 feet. It is fortunate that *Pinus* spp. are immune to attack except in the case of very old dry wounds. This immunity is the result of high resin exudation from the cut surfaces of living wood, which forms a protective covering on wounds which cannot be penetrated by the Cerambycid larvae.

A number of surveys have been carried out in recent years both in natural forest and in *Cupressus* and *Juniperus* plantations to obtain comparative information on the incidence of *Oemida gahani* in indigenous host species and plantation species in different forest areas.

Since the recognition that this pest was of importance during the post-war period, information on its depredations in *Cupressus* plantations has been collected at sawmills and in plantations by the examination of the cut ends of Cypress logs and where possible logs after sawing. The accumulated results have shown that the degree of attack is significantly different in forest areas on different sides of the Rift Valley, which bisects the main highland forest areas of Kenya. Thus, while nearly 75% of plantations sampled West of Rift were found to be attacked only 28% were East of Rift. Similarly, in the main Cypress growing areas West of Rift the overall rate of attack of trees in plantations is between 10 and 20%, while East of Rift it seldom exceeds 5%. The highest attack recorded—76% of trees in a plantation, was in the former region, and this gave a 30% degrade in the timber produced.

In order that a quick comparison of attack in *Juniperus* plantations in all forest areas could be obtained, a sequential sampling system was developed, which reduced the labour needed to obtain a useful result. Some 220 plantations varying in age from 10 to 50 years were sampled, about half on each side of the Rift Valley. This confirmed the *Cupressus* results, for the percentage of plantations showing significant damage West of Rift was more than twice that for East of Rift.

Widespread sampling of indigenous stumps and dead trees, which were in the past left in large numbers in plantation areas, have shown that the incidence of the pest in its natural hosts is much lower in East of Rift areas, and this appears to be due to the comparative rarity in those areas of a number of species most commonly attacked West of Rift. In fact, of the 20 or so preferred species present, 6 generally occur only in small numbers East of Rift. The composition of the natural forest would therefore appear to be the most important factor affecting the incidence of *Oemida gahani* in different parts of the Kenya highland forest areas.

Though indigenous stumps are the greatest danger in Cypress plantations as reservoirs of the pest, recent sequential sampling of old Cypress thinnings has shown that contrary to previous opinion, thinnings of up to 12 years felled may still harbour it in large numbers. Despite the majority of the logs being more than 50% rotten, many still support the active borer in small areas of sound wood. *Oemida* will not bore in rotten wood.

The basic method of controlling this pest by the removal of indigenous stumps from planting areas, usually by burning, before planting, should ideally be augmented by the removal of thinnings. This is impracticable in the case of unsaleable thinnings of age 11 to 13 years and it is probable that the treatment of pruning wounds with long lasting greases will have to be enforced in such plantations in high *Oemida* incidence areas, to prevent oviposition. The reduction in size of pruning scars to enhance rapid occlusion, by early and frequent pruning will also be essential.

During the last few years a number of cases have been discovered of attack of living and healthy *Cupressus* trees by another common indigenous Cerambycid borer—*Cholrophorus carinatus* Aur. This insect normally bores beneath the bark of recently dead trees and logs and penetrates the sapwood in which it finally pupates. It has apparently adapted itself to life in living sapwood into which it penetrates from the dead wood of old wounds produced either by animals (rats), disease (canker) or pruning. Pupation also takes place in the living sapwood and the beetle emerges through the bark. This insect may well be a potentially serious pest of *Cupressus* species and could eventually cause damage to sapwood, equivalent to that caused to the heartwood by *Oemida gahani*. It would seem however, that similar methods of control to those recommended for this pest would be as effective for *Chlorophorus*.

*All these pests are potentially dangerous, particularly as the exotic plantation areas are expanded.

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TYPES OF AMBROSIA BEETLE ATTACK ON LIVING TREES IN TROPICAL FORESTS

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The circumstances in which ambrosia beetles of the families Platypodidae and Scolytidae infest living trees in tropical forests may be classified in five distinct categories, each of which poses its own problems in forestry practice.

(1) Habitual and persistent attack on apparently healthy trees of a limited number of species. The only ambrosia beetles at present known in this category are the Platypodids *Dendroplatypus impar* (Schedl), which breeds in certain *Shorea* spp. (Dipterocarpaceae) in western Malaysia, and *Trachyostus ghanaensis* Schedl, breeding in *Triplochiton scleroxylon* (Sterculiaceae) in West Africa (Ghana to Sierra Leone). Infestation is apparently not seasonal, or connected with any marked decrease of the vigour of the tree.

(2) Sporadic mass attacks on apparently healthy trees. The only known example in this category is the Platypodid *Doliopygus dubius* (Samps.). It is normally a borer of logs of many species, but large numbers of the beetles frequently attack living and apparently healthy trees of *Terminalia superba* (Combretaceae) in parts of West Africa. There is some reason to suppose that there may be resistant strains of the host species, and this requires further investigation.

(3) Attack on many tree species when their vigour is temporarily reduced. Numerous species of ambrosia beetle have been recorded in this category, typically attacking during the dry season or during unseasonable droughts. The importance of this type of attack, especially in forests where there is a pronounced dry season, and its possible control, require investigation.

(4) Attack through wounds. This type of attack is localised and, in the absence of other factors of predisposition, such as drought, seems invariably to fail. It is normally of little or no importance.

(5) Attack on very unhealthy and dying trees. Infestation is often heavy, and where such trees are numerous, e.g. following a poisoning of weed trees prior to commercial fellings, may result in a large and rapid build-up of the ambrosia beetle population with a consequently increased hazard to commercial trees cut in the subsequent felling. This hazard, however, may be eliminated by correct timing of the two operations of poisoning and felling, as the population build-up is followed by an equally rapid decline. There is also some danger that the increased ambrosia beetle population may attempt attack on healthy living trees. Except in the case case of *Doliopygus dubius*, however, any such attempted attack is certain to result in failure unless it coincides with the dry season, and here again correct timing is necessary.

The practice of girdling or poisoning trees prior to felling, in order to lighten the wood for the purpose of extraction by water, might also be considerably extended were it not for the danger of attack by ambrosia beetles and other borers. At present there is no practicable method of overcoming this difficulty.

TERMITE DAMAGE TO PLANTATION-GROWN HOOP PINE IN NEW GUINEA

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Bulolo, situated about 40 miles from Lae, New Guinea, is an important centre for plywood production using peeler logs of klinki pine (*Araucaria hunsteinii*, K. Schum.) from neighbouring prime forests. In order to ensure continuity of log supplies an active programme of re-afforestation has been undertaken, but because of low viability and availability of klinki pine seed, the replanting has been done with hoop pine (*Araucaria cunninghamii* Ait.).

Early in 1961 isolated trees and small groups of trees in plantations were found to be dead or dying and subsequent examination established that these losses were due to attack by

Coptotermes elisae (Desneux). A survey of some 2000 acres of plantations showed that groups of affected trees were invariably associated with rotting stumps which survived clearing and burning operations, and the presence of termites in plantation trees was indicated by mud-covered runways or plastering on the basal portions of the trunks. By 1963 the infestation level had reached 7·2% in at least one compartment, and trees in all age groups from 3 years to 13 years old showed evidence of attack.

In the early stages of attack, trees show external mud-covered runways and there are relatively few internal galleries and no mud packing. Later on the lower trunk is completely sheathed in mud and internally there is extensive hollowing accompanied by mud-packing and the development of a nest-like structure. Affected trees firstly show loss of colour from the foliage and wilting and subsequently are prone to wind-throw because of the weakening of the trunk.

C. elisae occurs normally in the prime forest and appears to prefer klinki pine as a host tree. Mature colonies in such situations may survive clear felling and burning operations which precede plantation establishment, and it is these colonies, probably as a result of food stress, which are responsible for the attacks on young plantation trees. This explanation fits the observed pattern of attack which consists of small groups of trees sporadically distributed throughout the plantations, and generally closely associated with an old rotting stump.

There are two approaches to control, firstly by treating the young plantation trees, and secondly by destroying the residual mature colonies. Treatment of infested plantation trees by injecting 0·03% dieldrin emulsion into the gallery system within the trunk has been successful, but attempts to protect sound trees by applying 1-2 pints of the same emulsion to the soil around the base of the tree have failed completely, most probably because invasion commonly occurs through deep lateral roots below the level of treatment.

Efficient and economic destruction of residual colonies appears possible by injecting arsenical dusts into the gallery systems. The main difficulties are locating infested stumps in dense vegetation and rugged terrain, and successfully introducing the poison dust in large infested stumps or logs which may be up to 5ft. in diameter. There is good reason to believe that these problems can be overcome with the consequent elimination of termite damage to young plantation trees.

PRESERVATIVES AGAINST WOOD-BORING INSECT ATTACK

RECENT ADVANCES IN CHEMICAL INSECT CONTROL FOR PROTECTING STORED WOOD IN FORESTS

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Since 1937 preparations containing arsenic have been tested to protect unbarked timber from insects. All sides of logs were treated and they were then stacked in tight piles and covered with brushwood and moss. Sodium arsenite proved to be the only satisfactory insecticide, but arsenic preparations, especially the easily soluble salts, had a marked stimulative effect on the spread of blue-stain fungi, reducing timber quality. Blue-stain fungi were reduced considerably and insect pests were kept within tolerable limits by using less soluble salts (e.g. zinc arsenate). Spruce brush provides protection against rain only for a limited period and moss is difficult to lift from frozen ground in the spring. Experiments showed that tar-oil impregnated board gave completely satisfactory protection without increasing costs to any appreciable extent and was regularly used in experiments up to 1950 when Gesarol 50 and other rain-resistant preparations came on the market.

During the war arsenic preparations were replaced by synthetic insecticides, firstly DDT and later BHC and many others. Experiments with DDT showed that suspensions, emulsions and oil solutions were effective while powders were not; good results were obtained with 1% suspensions and oil solutions and 0·5% emulsions. However, with the exception of oil solutions the final effect of the preparation was dependent on the protective covering.

Other synthetic insecticides (γ-BHC, parathion, chlordane, dieldrin etc.) have been tried alone and in combination with varying results. Preparations based on these have been developed by industry to give adequate protection, combined with properties such as wetting, spreading, adherence, persistence, etc.

The problem of protecting unbarked wood against insect attacks was solved at an early stage but, for practical purposes, preparations were necessary which were effective after the insects were under the bark or had penetrated into the wood. It was important to increase the very short period available between snow melting and swarming of the bark beetles. A preparation with a minimum surface tension and with an effective fumigant as an additive was needed. Tests in the spring of 1958 about a fortnight after the main swarming of pine bark beetles showed that almost 100% effect was obtained with the preparation Xylamon GI/lindane + dieldrin/, Witoxyl/lindane + different fumigants/ and Timolan/lindane + DDT/, with fuel oil or petroleum as solvents.

Early experiments with logs treated individually and on all sides were costly and required much labour. Tests were made in 1958 to find out whether surface spraying of all accessible parts of the piles could provide sufficient protection and which type of spraying equipment would be suitable for the purpose. The tests involved 22 piles of 15 pine logs on average 5m^3 piles measure and stacked identically. The piles were sprayed before swarming period with 2% Xylamon GI using (1) a knapsack sprayer ("Senior), (2) a portable power sprayer ("Fontan") and (3) an aerosol generator ("TIFA") as follows:

Type of equipment	*Dosage rate, l/pile*	*Insect attack, %**
Senior	2	6·6
Senior	3·5	1·6
Senior	5	1·0
Fontan	2	3·6
Fontan	3·5	1·1
Fontan	5	0·8
TIFA	2	19·8
TIFA	3·5	7·4
TIFA	5	15·2
Untreated piles	—	50·7

*area covered by insect galleries in relation to the total surface.

From this it can be seen that the best results were obtained by using the power sprayer equipment, somewhat less good results were given by the knapsack sprayer, while the aerosol generator was considerably less effective.

A more comprehensive picture is given of the effect of the different sprayers if the insect attack on the different layers of the piles are set out in order:

Type of equipment	*Insect attack (%) in*		
	outer layer	*middle layer*	*bottom layer*
Senior	3·0	2·8	3·4
Fontan	2·3	1·4	1·3
TIFA	16·2	13·5	6·3
Untreated piles	59·3	44·2	36·7

This shows:

(a) the knapsack sprayer provides rather better protection to the outer layer than to the middle or bottom layers but the difference is of no practical significance.

(b) the Fontan equipment provides nearly equal protection to all layers.

(c) the aerosol generator gives its best protection to the bottom layer but even here the effect is unsatisfactory.

A dosage of 3·5 litres of liquid (700 ml/m³ piled measure and 60 ml/m² of bark surface) was quite satisfactory for both the portable type of sprayers but not for the TIFA aerosol generator.

Experiments were carried out in 1961-2 with pine divided into piles of thin and thick-barked logs in order to investigate the importance of concentration and dosage rate; in 1961 Xylamon GI (oil solution) was used and in 1962 Xylamon FK (emulsion). Different concentrations and dosages were used before and after the swarming of bark beetles. The most remarkable result of the 1961 experiment was that the concentration could be reduced from the manufacturer's recommended 2% to 0.25% without greatly impairing the effect, provided that the dosage rate prior to bark beetle appearance was maintained at a minimum of 150 ml/m² for thick-barked and 100 ml/m² for thin barked logs.

After the beetles had swarmed the thick-barked logs needed 250-300 ml/m² in a concentration of not less than 0·5%.

Similar results were obtained in the 1962 experiment with the preparation emulsified in water. The dosage necessary was naturally higher, 250 ml/m² for thick-barked and 150 ml/m² for thin-barked logs.

In 1963 in connection with the dosage values obtained, tests were carried out with other preparations, including 2% Timolan (emulsion and oil solution), 1-2% Witoxyl (emulsion and oil solution) and 0·2% malathion (emulsion). The first two in oil solution gave satisfactory results both before and after the swarming, but the emulsions only before the swarming. Malathion was completely ineffective.

Another matter of interest for green wood protection is duration of persistence of the chemical preparations. A partial answer to this question is provided by tests made in 1962. Thick and thin-barked spruce and pine logs were placed in single-layer piles and sprayed in the late autumn of 1962 with 1-2% Xylamon (emulsion and oil solution), with dosage rate 50% higher than the previously obtained minimum values. The timber was left on the ground and examined the following autumn. No attacks by insects could be found in the treated piles, while controls were covered with galleries to approx. 45% of the surface area.

There is now a tendency to centralise the barking of pulp wood at pulp mills, which means that it lies unbarked in the forest for up to a year, providing excellent conditions for insect pests with resulting attacks on growing trees. Treatment of stored unbarked pulp wood with chemicals is thus essential and in 1963 a series of tests on a large scale were carried out using several chemical preparations. A large number of stacks of approx. 10 m³ pulp wood was treated before the swarming using a power sprayer (Fontan) using both emulsions and oil solutions. Completely satisfactory results were obtained with 2% Timolan emulsion, 1% Witoxyl emulsion and oil solution and 1% Xylamon emulsion and oil solution. The minimum dosages were 0·6-0·7 litres/m³ piles measure for oil solutions and 1 litre/m³ for emulsions. A knapsack sprayer (Senior) gave poorer results than the power sprayer.

The cost of spraying pulp wood is approx. 30 Swedish öre (5d.) per m³ piled measure, the chemical accounting for one third of the cost.

DIE WIRKSAMKEIT VON SCHUTZMITTELN GEGEN HOLZZERSTÖRENDE KÄFER UND IHRE BESTÄNDIGKEIT

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Unter den holzzerstörenden Käfern sind in Europa *Hylotrupes bajulus* L., der Hausbockkäfer, *Anobium punctatum* De Geer, der Gewöhnliche Nagekäfer, und die *Lyctus-Arten*, die sog. Splintholzkäfer, die bei weitem wirtschaftlich wichtigsten. Alle vermögen sich in lufttrockenem Holz zu entwickeln, und sie sind nicht auf einen vorangehenden Pilzbefall angewiesen.

Das Holz als Werkstoff, in dem bereits vorhandene Schädlinge *bekämpfend* abgetötet oder von dem sie *vorbeugend* ferngehalten werden sollen, stellt besondere *Anforderungen an die Schutzmittel.* Abgesehen von ihrer Wirksamkeit müssen sie leicht in genügender Menge und hinreichend tief in das Holz einzubringen sein, und sie müssen eine Reihe technischer Eigenschaften gegenüber Werkstoffen besitzen sowie die erforderlichen hygienischen Anforderungen erfüllen. Schießlich wird von den Holzschutzmitteln eine lange Wirksamkeitsdauer erwartet.

Wegen dieser vielfältigen Anforderungen hat sich nur eine *Auswahl von Stoffen* als Hauptbestandteile von *Holzschutzmitteln* gegen Insekten bewährt. Dies sind unter den wasserlöslichen Verbindungen zum vorbeugenden Schutz für Holz unter Dach in bewohnten Räumen Hydrogenfluoride, Fluorosilikate, Chromat-Hydrogenfluorid-Gemische und Bor-Verbindungen, für Holz im Freien Gemische von Chrom-Verbindungen und Verbindungen von Fluor, Fluor und Arsen, Kupfer, Kupfer und Arsen oder Kupfer und Bor. Ölige Holzschutzmittel enthalten Teeröle und Teeröl-Fraktionen, chlorierte Naphthaline, Mineralöle verschiedenen Typs sowie in den letzten Jahren fast ausnahmslos auch synthetische Kontaktinsektizide. Für Holz im Freien, besonders Leitungsmaste, wird nur Steinkohlenteeröl bestimmter Qualität verwendet.

Zur Prüfung und Beurteilung der Wirksamkeit der Holzschutzmittel gegen Insekten dienen in Deutschland drei genormte Verfahren (DIN 52 163, DIN 52 164 und DIN 52 165). Für die Prüfung der *Beständigkeit der Wirksamkeit* auf Abgabe flüchtiger Bestandteile (sog. Verdunsten oder Verdampfen) und durch Auswaschung (vor allem durch Regen) bestehen Verfahren, die z.T. genormt sind.

Ergebnisse einer vergleichenden Giftwertbestimmung mit Hausbock-Eilarven sind in der Form zusammengestellt daß zum Vereinfachen einer Ubersicht die zum sicheren Abtöten aller Larven nach 12wöchiger Versuchsdauer, die weit über die Hungerfähigkeit von 3 bis 4 Wochen (unter den gegebenen Versuchsbedingungen) hinausreicht, erforderlichen Salz- oder Ölmengen in abgerundeter Form angegeben werden. Die Werte sind nach 4 wöchiger Lagerung des behandelten Holzes bis zum Einsetzen der Tiere in das Holz gewonnen.

Die Giftwerte für Hydrogenfluoride und Fluorosilikate mit rund 300 g je m^3 Holz liegen etwas niedriger als der Wert von rund 400 g für Bor-Verbindungen und von rund 500 g für Chrom-Fluor- und Chrom-Fluor-Arsen-Gemische. Die Chrom-Kupfer-Gemische sind wesentlich weniger giftig. Während bei diesen wasserlöslichen Salzen die Giftwerte innerhalb einer Zehnerpotenz liegen, gibt es bei den öligen Holzschutzmitteln in Abhängigkeit vom Gehalt an Kontaktinsektiziden Unterschiede zwischen rund 30 kg je m^3 Holz bei Steinkohlenteeröl oder etwa vor 2 Jahrzehnten üblichen Hausbockbekämpfungsmitteln und Giftwerten in der Größenordnung von 50 g je m^3 Holz bei neuen Präparaten, also in einem Verhältnis von rund 1000:1. Die Giftwerte für Kontaktinsektizide selbst liegen nach 4wöchiger Lagerungszeit des behandelten Holzes bis zum Einsetzen der Tiere noch um weitere 1 bis 3 Zehnerpotenzen tiefer als der für die sehr wirksamen Handelsschutzmittel angegebene Wert.

Die Giftwerte von chromhaltigen Salzgemischen nach dem genormten Auswaschversuch befinden sich (mit Ausnahme eines älteren Salz-Typs) zwischen 2 und 3 kg je m^3 Holz. Diese Werte sind niedriger als die Grenzwerte für einen Schutz gegen holzzerstörende Pilze. Da diese für Holz im Freien die wichtigeren Schädlinge sind und gegen sie auch ein bestimmter Erfolg der Anwendungstechnik unerläßlich ist, bedarf es keiner weiteren Diskussion der Insektengiftwerte der Salzgemische.

Anobien-Eilarven sind giftempfindlicher als die viel größeren Hausbock-Eilarven. Schutzmittel, die gegen letztere ausreichend vorbeugend wirksam sind, müssen sich auch gegen Anobien bewähren.

Über die Frage der *Beständigkeit der Wirksamkeit* liegen jetzt Ergebnisse langfristiger Versuche vor. Daß die Giftwerte für Hydrogenfluoride, Fluorosilikate und sogar für Fluor- und Chrom-Verbindungen enthaltende Gemische nicht beständig sind, beruht auf einer Fluorwasserstoff-Abgabe aus dem Holz in Dampfform. Nach ungefähr 6 bis 18 Monaten wird ein sich dann nicht oder kaum mehr ändernder Endzustand des Fluor-Gehalts erreicht, mit dem offenbar für Jahrzehnte gerechnet werden kann. Bisher liegen chemische Analysen und Erprobungen in dem praxisnahen Versuch auf einem Dachboden mit der Hausbock-Eiablage an Kantholz-Abschnitten für 10 bis 12 Jahre Probenlagerung vor.

Unerwartet war die verhältnismäßig große Beständigkeit von Kontaktinsektiziden im Holz. Noch nach 10jähriger Lagerung behandelter Holzproben bei 20° C reichen bei einigen besonders wirksamen und beständigen Verbindungen Einbringmengen von 1 g oder weniger je m^3 Holz zu einem Schutz gegen Hausbock-Eilarven aus, und der Faktor der Wirkungsabnahme liegt, von γ-HCH abgesehen, unter 10.

Die lange Dauer der Wirksamkeit ist für den *vorbeugenden Schutz* unentbehrlich. Von gewissen öligen Holzschutzmitteln des Handels mit einem Gehalt an geeigneten Kontaktinsektiziden reicht eine Aufbringmenge von 150 . . . 200 g je m^2 Holzfläche aus, um noch nach 10 Jahren Dachboden-Lagerung ein Einnagen der Hausbock-Eilarven durch die behandelte Schicht zu verhindern. Dies war bei älteren Präparaten ohne Kontaktinsektizide nicht der Fall gewesen.

Ein Sicherheitsfaktor ist wegen der natürlichen Streuung der Flüssigkeitsaufnahme durch das Holz erforderlich. Von wasserlöslichen Holzschutzmitteln sollten nicht weniger als 50 g Salz je m^2 Holzfläche angewandt werden. Ölige und wasserlösliche Schutzmittel sind in zwei Arbeitsgängen aufzubringen, damit eine gleichmäßige Holzbehandlung besser gewährleistet ist.

Besondere Anforderungen an die Schutzmittel-Eigenschaften stellt die *Bekämpfung holzzerstörender Insekten* in befallenem Holz. Gutes Eindringvermögen in Holz und von Bohrmehl angefüllte Fraßgänge der Flüssigkeiten, Wirksamkeit gegen die Insektenlarven und -puppen, möglichst in Gas- oder Dampfform über den von der Flüssigkeit durchsetzten Bereich hinaus, und langanhaltende vorbeugende Wirkung sind entscheidende Voraussetzungen.

Bei der Giftempfindlichkeit von größeren Hausbock- und Anobienlarven gegenüber Kontaktinsektiziden besteht ein bemerkenswerter Unterschied darin, daß die letzteren gegen Phosphorester-Präparate empfindlich und gegen verschiedene chlorierte Kohlenwasserstoffe widerstandsfähig sind, bei den Hausbocklarven das Verhältnis aber umgekehrt ist.

Übliche Aufwandmengen für die Bekämpfung holzzerstörender Insekten sind bei Hydrogenfluoriden 100 g Salz, bei öligen Präparaten 300 bis 500 g Öl je m^2 Holzfläche.

Während der Erfolg einer Bekämpfung nach verhältnismäßig kurzer Zeit beurteilt werden kann, pflegt der Bewährungsfall für den vorbeugenden Schutz meist überhaupt erst nach Jahren einzutreten. Hier ist sorgfältige und verläßliche Arbeit besonders wichtig. Für eine *Gütekontrolle der ausgeführten Holzschutz-Arbeiten* sind in den letzten Jahren die erforderlichen Voraussetzungen erarbeitet worden, und Richtlinien für ihre Durchführung bestehen bereits (DIN 52 161, mehrere Blätter) oder werden vorbereitet.

Abschließend läßt sich feststellen: Seit der Zeit des 7. Entomologie-Kongresses in Berlin vor einem Vierteljahrhundert und des 9. Kongresses in Amsterdam im Jahre 1951 sind die wissenschaftlichen Grundlagen des Holzschutzes beträchtlich erweitert und ist die Wirksamkeit von Schutzmitteln gegen holzzerstörende Käfer erheblich gesteigert worden. Es gibt viele Präparate mit ausgezeichneter Bekämpfungs- und vorbeugender Schutzwirkung. Die letztere hat sich bei den meisten gegenwärtig amtlich anerkannten Präparaten als sehr beständig erwiesen. Die Wirkungsdauer ist für Beispiele aller Schutzmittel-Typen für mindestens 10 Jahre nachgewiesen und reicht sicherlich noch länger. Worauf es jetzt ankommt, ist eine dem Umfang der Schädlingsausbreitung und des Schadens angemessene, sachgemäße und sorgfältige Anwendung der Schutzmittel.

USE OF A LATIN SQUARE DESIGN FOR CONSIDERATION OF SEVERAL FACTORS IN TESTING OF WOOD PRESERVATIVES

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At the Government Pest Infestation Laboratory in Denmark we test preservatives at the request of the manufacturers in order to give an official recognition if they are found satisfactory.

In our test method we have always aimed at testing the effect of ageing on the toxicity of the treated wood rather than the momentary toxic value. We have also found it necessary to prescribe rather high amounts of preservative, 1 litre per m^2, solely in order to ensure a sufficient coverage and penetration.

These points of view are motivated by the fact that the larvae being deeply confined in the wood are in practice inaccessible to the penetrating preservative and to control them it is necessary that the preservative retains its effect until the insects come into the treated zone. As a further security it is important also that the preservative is effective long enough to prevent the establishment of newly hatched larvae of the next generation which might come from beetles hatched from larvae surviving in less well treated parts of the timber.

On the other hand, if the effect of the preservative diminishes only slowly, within wide limits the absolute value of the initial toxicity is not very critical.

A test method based upon these principles but including an unrealistic mode of impregnation was based upon a 5×5 latin square design. The three orthogonal factors were: size of the larvae, uptake by the blocks, and storage time of the impregnated blocks. The larvae were arranged in groups of size with the averages of the groups distributed with logarithmically equal distances between 20 and 200 mg. The 25 blocks were selected out of 50 blocks impregnated by dipping for 15 minutes so that the averages of the uptake in the five groups were most widely distributed and the blocks were as uniform as possible within the groups. The lengths of the storage times were distributed with logarithmically equal distances between 10 days and 720 days.

In each block two larvae were inserted of the size group predicted by the design to be combined with that uptake group to that storage time. The two larvae were replicates within the design which had thus 25 degrees of freedom for the estimation of the random sampling error.

The reciprocals of the survival times in days were used as the response, as they gave a rather normally distributed measure of the toxicity, at least within each type of preparation.

By means of this design two new contact insecticide preparations were compared with an old one in three random squares, and the analyses of variance according to the latin square design gave means to segregate between the effects of larval size, of uptake in the blocks, and of storage time. The effect of the storage time was analysed further with polynomial coefficients and it was possible to demonstrate that the effect of the old preparation diminished with a constant percentage loss whereas the new preparations tended to stabilize at a certain toxicity after about one year of storage. On this basis, and not on the basis of the average toxicity the two new preparations were concluded to be better than the old one.

Also the effect of pressure impregnation with a salt preparation was tested according to this design and in spite of the low initial toxicity the preparation was concluded to have a very good effect because it was completely unchanged during the storage. Unfortunately practical difficulties limit the use of this method for the control.

The shortcomings of this test method lie in the necessity of using big larvae and the mode of impregnation. Because of impregnation by dipping, the distribution of the preservative in the wood is unlike the distribution following the normal spraying, and the distribution in the wood interacts seriously with the rate of deterioration of the effect by storage. This is partly overcome by comparisons using the same preservative or with very similar preparations, but it is important if very different preservatives are to be compared.

On these grounds a new method of test is being developed. It is based upon the impregnation of small blocks in a way simulating the spraying performed by practical operators. On to these blocks egg larvae are put according to the method outlined in the German DIN

52621. The percentage of larvae failing to establish themselves is used as a measure of mortality. In order to observe the effect of storage the preservative is used in dilutions about the LD 50 and the rate of deterioration of the effect is measured by the rate with which the LD 50 moves towards higher initial doses as the result of different lengths of storage.

SOIL INSECTICIDES FOR PREVENTION AND CONTROL OF SUBTERRANEAN TERMITES IN BUILDINGS

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Field studies have been in progress in south Mississippi since 1944 to determine the effectiveness of chemicals applied to the soil for the prevention and control of subterranean termites in buildings. The plots are in a pine-hardwood forest on a light, sandy loam soil having a pH of 5·3 to 5·5. Rainfall averages approximately 70 inches per year. *Reticulitermes virginicus* (Banks) and *R. flavipes* (Kollar) occur in the area.

The objective of soil treatment is to establish a barrier through which termites will not pass. This barrier is particularly valuable under buildings on concrete ground slabs, because such buildings are very vulnerable to termite attack.

Two test methods are used. They are designed to simulate in certain respects (1) the application of chemicals to the soil prior to pouring concrete slabs in building construction, and (2) trench treatment along the foundations of buildings. In both methods, termites must penetrate chemically treated soil before they can attack a piece of susceptible wood.

In studies still in progress, 100 per cent protection has been maintained with 1·0 per cent chlordane for 15 years, with 0·5 per cent aldrin or 0·5 per cent dieldrin for 14 years, and with 0·5 per cent heptachlor for 11 years. The chemicals were formulated as water emulsions and applied at the rate of 1 pint per square foot of soil surface. The maximum period of protection that the formulations will give is unknown. Since 1958 granular formulations of these chemicals have been in test. They have so far been 100 per cent effective where applied to the soil surface.

Benzene hexachloride, 0·8 per cent gamma in water emulsion, and 8·0 per cent DDT in oil failed after about 10 years. The duration of protection depends to some extent on the quantity of chemical applied. Thus, 4·0 per cent DDT, applied at the rate of 2·5 gallons per 10 cubic feet of soil, was 90 per cent effective for 6 years and 70 per cent for 7 years; at the same rate of application 8·0 per cent DDT was 90 per cent effective for 11 years and 70 per cent for 12 years. Once failures begin, they generally increase rapidly. To illustrate, 8·0 per cent DDT was only 10 per cent effective after 14 years. Since the cost of the chemical is a small part of the total cost of treating a building, it is false economy to reduce the quantity applied.

VERFAHREN ZUR BESCHLEUNIGTEN ZÜCHTUNG DES *ANOBIUM PUNCTATUM* IM LABORATORIUM

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Lange Entwicklungszeiten und Schwierigkeiten bei der Aufzucht des Holzschädlings *Anobium punctatum* De Geer wirken sich bisher auf biologische Untersuchungen und Prüfarbeiten an Bekämpfungsmitteln hemmend aus.

1. ÜBER DAS ZUCHTMEDIUM. Es wurde nunmehr gefunden, daß eine stark beschleunigte Entwicklung in einem Backwerk aus 32 Teilen Nadel- oder Laubholzmehl, 9 Tl. Zellulose-

flocken, 11 Tl. Stärke, 16 Tl. Bluteiweiß und 32 Tl. Bächerhefe erzielt wird. Aus den Bestandteilen wird mit Wasser ein Teig hergestellt, der nach Trocknung in Warmluft (60°C) nach Belieben geformte holzähnliche Körper ergibt.

Die Anwendung von Hefe und Kohlehydrat geht auf die grundlegende Untersuchung der Ernährungsphysiologie durch Becker (2) sowie die Darmenzymbefunde von Parkin (8) zurück. Bluteiweiß und Stärke bewirken den holzähnlichen Zustand des Backwerkes; Bluteiweiß fördert zudem die Larvenentwicklung (5).

Von einer Anzahl verschieden geformter Körper bewährte sich am besten der "Synthesehohlblock". Zu seiner Herstellung wird der Teig in quadratische Formrahmen, 8 x 8cm, Höhe 3 cm, rund um einen Trichter eingepreßt. Nach der Trocknung wird die große Öffnung mit einer durchbohrten Plexiglasscheibe abgedeckt, die kleine Öffnung sowie die Bohrung der Deckscheibe (Durchmesser 2 cm) mit Gaze verklebt.

Der Synthesehohlblock stellt so ein Gefäß zur Aufnahme der Käfer dar, das gleichzeitig als Eiablageplatz sowie als Nahrung für die Larven dient. Die Fehlorientierung der Käfer durch Licht und thigmotaktischen Reiz in Glasgefäßen wird vermieden. Die schräge Innenfläche gestattet die Beobachtung der Eiablagen unter dem Binokular. Dem von Cymorek (4) beschriebenen Sterzelverhalten der Weibchen und seinem Zweck, Anlockung der Männchen, kommt die Durchlüftung des Innenraumes entgegen; sie fördert Luftaustausch und Klimatisierung des Materials.

Einschnitte und Perforationen auf der Innenfläche erhöhen deren natürliche Attraktivität für die Eiablage. Auch die Verfahren von Kelsey (6), Bletchly (3) mit Musselinstreifen und Spiller (9) mit Einprägungen sind anwendbar.

2. ZUCHTERGEBNISSE.

2·1 Die Zucht in Synthesematerial wird seit 2 1/2 Jahren durchgeführt und enthält in einem Teil die 3. Generation. Die natürliche Entwicklungsdauer von 2-4 und mehr Jahren ist auf 8-11 Monate verkürzt; Käfer werden auch außerhalb des natürlichen Schlupftermines erhalten.

Die Larven der 2. Generation ließen in ihrer Giftempfindlichkeit keinen Unterschied zu Freilandmaterial erkennen. Die Überprüfung erfolgte in Holz nach DIN 52 165 mit Lindane und Phosphorsäureester. Die Entnahme der "vergleichbaren" Larven für Testzwecke wird durch die geringere Festigkeit der Synthesehohlblöcke und den Individuenreichtum sehr vereinfacht. Eine Einteilung der Prüftiere nach Größen ist weiterhin erforderlich, da sich nicht alle Larven gleich schnell zu entwickeln vermögen.

Einer maximalen Klimatisierung der Zucht (2) stand bisher das Auftreten von Schimmelpilzen und Milben entgegen. Die Zuchtkörper wurden daher nach dem Einbohren der Eilarven bei 22°C, 95% rel. in einem Raum bei 70% rel. freistehend aufbewahrt und durch Besprühen zusätzlich befeuchtet. Durch Konservierung und die Isolierung der Zuchtkörper mit Sperrflüssigkeiten wurde neuerdings eine erhebliche Verbesserung erzielt.

Bei optimalen Klimaverhältnissen ist eine weitere Entwicklungsbeschleunigung zu erwarten.

2.2 Die Möglichkeit, die Methode an die Bedürfnisse anderer Arten anzupassen (Mitverwendung von Faulholz, Pilzkörpern, getrockneten Pflanzen, Wolle usw.), legt Zuchtversuche mit Vertretern verschiedener Ordnungen und Familien nahe.

Aus Zuchten mit 20 Xylophagen liegen vorerst folgende komplette Entwicklungen vor:

Art	*Stärke-gehalt*	*Klima*	*Käferschlupf, Tage nach Einsetzen der Elterntiere*
Lyctus brunneus Steph	3-fach	25°C, 65% rel.	65
Dinoderus minutus F.	5-fach	25°C, 65% rel.	60
Ernobius mollis L.	normal	21°C, 75% rel.	81

Lyctus brunneus legte Eier in Risse des Synthesehohlblockes und erweist sich somit als 2. *Lyctus* Art (1, 7), bei der für die Eiablage keine absolute Bindung an Holzzellen besteht.

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VERY HIGH FREQUENCIES AND WOOD-BORING INSECT CONTROL

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Research into alternative methods of treating insect-infested wood when the traditional ways employed in the United Kingdom (e.g. application of liquid insecticides or fumigation with toxic gases) are impracticable, has involved studies on the value of VHF radio waves (2,450 Mc/s). Both HF and VHF radiation kill insects by thermal effects. Investigations by Becker and Loebe (1961) showed that in relatively dry atmospheres, larvae of *Anobium punctatum* De G. were killed by temperatures of 55°C for 30 minutes or 58°C for 20 minutes produced by conventional methods. Parkin (1937) found that when humidities were high, lower temperatures could be employed effectively. Neither in previous studies by Thomas and White (1959) on HF, nor in the current studies on VHF, were differential heating effects detected, hence the effective temperatures are expressed as those obtained in the wood.

Using magnetron equipment, tests have been carried out on naturally infested birch plywood boards made up with blood and casein glues. These $\frac{1}{2}$ inch thick boards were treated either singly or in sets of 8 or 9. The sets of boards were placed in a 2 inch thick redwood (Scots pine) box giving a total thickness of either 6 or $6\frac{1}{2}$ inches of wood (i.e. redwood and plywood) from the face nearest to the source of radiation to the plywood face furthest away from the source. Complete control was not achieved in the group of 8 boards, previously conditioned at 65 per cent RH, when heated from 32°C to 72°C over a 3 minute period. Heating the group of 9 boards, previously conditioned at 90 per cent RH, to 51°C over a 7 minute period was, however, effective, but since the number of test larvae was small, these results cannot be considered entirely reliable. Heating boards singly to a temperature of about 50°C after conditioning out-of-doors appeared to be effective. These results are similar to those previously obtained by Thomas and White (1959) for HF radio waves (37·5 and 76·0 Mc/s) using *Lyctus brunneus* Steph. as the test insect. However, to obtain definitive data on the precise temperatures required, and the time needed to achieve them in relation to the power output of the equipment and a range of moisture contents in wood, additional experiments would be necessary. Since only small areas of wood can be treated at one time, the costs are likely to be high; moreover, evidence of fire hazard was obtained in one test. Consequently, further tests are considered unjustified until more information is available on fire risks and the economics of this method of treatment.

It is possible that VHF radio waves might be of value for treating limited areas of deep seated infestation in wood where conventional methods of treatment might prove ineffective, or where structural weakness resulting from insect attack might be particularly significant. Hazards to human health during application of this type of radiation are likely to be low if appropriate precautions are taken, neither is there any significant risk of causing structural weakness to the wood itself over the short period of treatment normally needed. A possible method of preventing damage to surface finishes would be a combination of intermittent heating with superficial cooling using air supplied from a blower.

A more detailed account of this work is being published elsewhere.

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DIE POPULATIONSDYNAMIC DER FORSTINSEKTEN AUF DER RUSSISCHEN EBENE WÄHREND DER HUNDERT-JÄHRIGEN PERIODE

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Der Massenwechsel tritt am deutlichsten bei nadel- und blatt-fressenden Insekten auf. Die meisten dieser Insekten sind dadurch gekennzeichnet, dass sie auf den umfangreichen Territorien der Russischen Ebene zu Massenvermehrungen kommen.

Die Häufigkeit dieser über, ihr Vorkommen und ihre Entwicklung stehen mit dem Vorherrschen der einzelnen Typen atmosphärischer Zirkulation in engem Zusammenhang. Es sind 3 Typen atmosphärischen Zirkulation festgestellt worden: Westzirkulation (W), Ostzirkulation (E) und Meridianzirkulation (C).

In Abhängigkeit von den Forderungen jeder Art gegenüber den Verhältnissen der Umwelt bildet sich die jeweilige Reaktion auf die verschiedenen Typen der atmosphärischen Zirkulationheraus. Die Einwirkung der atmosphärischen Zirkulationsart auf die Population ist mannigfaltig und kann direkt und indirekt wirken. Bei der direkten Einwirkung fördern oder verhindern die Witterungsverhältnisse die Entwicklung, das Wachstum und die Ernährung der Insekten und andere biologischen Vorgänge. Dieselben Witterungsverhältnisse bestimmen das Mortalitätsniveau der Insekten durch physikalische Faktoren der Umwelt. Die indirekte Einwirkung der atmosphärischen Zirkulation wird durch die Ernährungs- und Habitätsverhältnisse in den verschiedenen Entwicklungsphasen durch die Entomophagen und Krankheiten bestimmt.

In Abhängigkeit von dem Niveau der Gradation können die Massenvermehrungen auf eine kleine Fläche begrenzt sein oder fast die ganze Russische Ebene befallen. Dabei, entsprechend dem Wechsel der atmosphärischen Zirkulationstypen und der Entwicklung der Zyklonenfronten, wird am häufigsten die Bewegung von Massenvermehrungen von Westen nach Osten beobachtet. Daraus erklärt sich ihre ungleichmässige Verbreitung in Bezug auf die über die Fläche. Diese Tendenz einer nicht gleichzeitigen Entwicklung verstärkt sich auch durch die lokalen Besonderheiten der Witterungs- und Landschaftstypen.

Wir haben die Analyse der Massenvermehrungen von 76 Arten nadel und blattfressender Insekten während der Hundertjährigen Periode auf Grund von statistischen Angaben und unseren eigenen Beobachtungen innerhalb der letzten dreissig Jahre angegeben.

Die kleinste Zahl der Massenvermehrungen fällt auf die Periode des Vorherrschens der Westzirkulation (1900-1928). Zu dieser Zeit wurde das massenhafte Auftreten nur der hygrophilsten Arten beobachtet. Innerhalb der Periode des Vorherrschens der Ostzirkulation zu Beginn des analysierten Jahrhunderts und später, während der Periode 1929-39, hatten die massenvermehrungen der xerophilen Arten die grösste Entwicklung bekommen, besonders *Ocneria dispar* L., *Dendrolimus pini* L., *Euproctis chrysorrhoea* L., *Panolis flammea* Schiff. So waren z.B. Massenvermehrungen von *Ocneria dispar* innerhalb zwei dreissigjähriger Perioden von 1867 bis 1896 und von 1929 bis 1959 zu beobachten. In beiden Fällen bewegten sie sich allmählich von der Steppen- und Waldsteppenzonen in die Waldzone durch die Migrationen der Falter in der Front entstehender Tiefenzyklone.

Die massenhaften Vermehrungen sind durch die extremen Abweichungen der einzelnen meteorologischen Elemente vom normalen Zustand und durch die anomale Entwicklung während einer Reihe von Jahren bedingt. Nach der Form ihrer Erscheinung werden solche Abweichungen am deutlichsten und mannigfaltigsten in der Periode des Vorherrschens der atmosphärischen Zirkulation der Typen E und C. Diese Periode (hauptsächlich von 1949-60) ist durch die grösste Vielfältigkeit an Arten von nadel und blattfressenden Insekten, die grosse Massenvermehrungen hatten, gekennzeichnet.

80% der Massenvermehrungen wurden durch epizootischen Krankheiten, besonders durch Polyedrose befallen. Das Erlöschen eines Anteils der Massenvermehrungen erklärt

sich durch die niedrigen Wintertemperaturen. Die Komplexe der Entomophagen unterdrückten, in der Regel, die Massenvermehrungen nicht völlig.

Die steigende Häufigkeit der Massenvermehrungen in den letzten 30 Jahren wird durch die zunehmende mannigfaltige Einwirkung des Menschen auf die Natur und durch schroffe Veränderungen der ökologischen Umwelt in vielen Waldmassiven bedingt.

HOLZSCHÄDLINGE IN DER TSCHECHOSLOWAKEI

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In den tschechischen Gebieten wurden in den Jahren 1959 bis 1963 die Untersuchungen der Artenzusammensetzung, der Intensität des Auftretens und der wirtschaftlichen Bedeutung der Holzschädlinge an den bei uns wichtigsten Holzarten, d. i. von den Nadelholzarten an der Fichte *Picea excelsa* Link. und der Kiefer *Pinus silvestris* L., von den Laubholzarten an der Sommereiche *Quercus robur* L. und den Pappeln *Populus* sp. vorgenommen. Das Untersuchungsobjekt waren vor allem die Lagerplätze im Walde, weiter stehende, namentlich durch Rauchgasemissionen geschwächte Bäume in dem Rauchschadengebiete vom Erzgebirge und an einer ganzen Reihe weiterer Lokalitäten auch durch bei uns häufig vorkommenden Hallimasch *Armillaria mellea* Vuill. geschwächte Nadelholzarten. Die eingehenden entomologischen qualitativen und quantitativen Analysen zeigten, dass wirtschaftlich bedeutsamer technischer Schädling des Fichten- und Kiefernholzes aller Dimensionen bei uns der gemeine Nutzholzborkenkäfer *Trypodendron lineatum* Ol. ist, bei dem die Befallsdichte namentlich des unentrindeten Materials in den Mengen 10 bis 20 Einbohrungen pro 1 dm^2 und Populationsdichte der im Boden winternden Käfer 100 bis 300 Stück pro 1 qm keine Seltenheit war. Mit Rücksicht auf die Bedeutung der Beschädigung wurde einerseits die Methode des Holzschutzes durch die Oberflächenbehandlung durch die Kontaktinsektizide auf der Basis DDT und BHC in den Emulsionsformen, andererseits durch die Bekämpfung des Schädlings im Laufe der Überwinterung im Boden durch die Desinfektion der Waldlagerplätze auf Grund der Anwendung von kombinierten Mitteln Orthodinitrokresol und Anthrazenöle erarbeitet.

Andere Schädlinge treten stark in den Hintergrund.

Das reichste Spektrum der Holzschädlinge wurde jedoch an dem Eichenholz festgestellt: an dem gefällten Holz aller Dimensionen entwickelten sich gemeinsam die Bockkäfer *Pyrrhidium sanguineum* L, *Phymatodes testaceus* F., *Plagionotus arcuatus* L., *Plagionotus detritus* L. und *Xylotrechus antilope* Schönh.

Die stärkstens vertretenen Arten *Pyrrhidium sanguineum* L. (28%) und *Phymatodes testaceus* F. (48%) nehmen im Durchschnitt etwa 3/4 der Durchschnittszusammensetzung ein, sind jedoch ohne wirtschaftliche Bedeutung, weil sie sich bei dem Eindringen in das Holz nur auf Splintteile begrenzen. Schwere Beschädigung des Eichenholzes wurde jedoch von beiden Arten der Gattung *Plagionotus*, deren Larvengänge bis in die Tiefe von 90 bis 100 mm eindrangen, verursacht. Trotzdem dass in der Totalzusammensetzung beide Arten die Vertretung nur von 11% darstellten, schied ihre schädliche Wirkung nicht selten bei der Manipulation wertvolle Sektionen aus den Lieferungen für die Schäl-, Textil- und Fassindustrie und sogar auch aus den Grubenholzlieferungen aus.

Die tschechoslowakischen Staatsstandarde, die die Bedingungen für die Klassifikation des Eichenholzes in die Sägesektionen und für Bauzwecke angeben, erlauben max. 10 Einbohrungen pro eine Länge eines laufenden Meters der Sektion: wir fanden in unseren Analysen, dass die Einbohrungszahl auf dem im Walde übergehend gelagerten Eichenholze sich von 0 bis 83 Einbohrungen bewegte und im Durchschnitt 28 Einbohrungen pro 1 l.m. betrug.

Diese Umstände führten uns zur Ausarbeitung eines verlässlichen Holzschutzes durch Oberflächenbehandlung mit Emulsionen, Kontaktgiften auf der Basis von BHC und DDT. Zugleich wurde versuchsweise auch in der älteren Literatur angegebene Bedeutung des Eichenholzlagerns in der Dauerbeschattung, sowie der präventive Holzschutz gegen die Beschädigung durch sonnenliebende Bockkäfer aus der Gattung *Plagionotus* überprüft.

Während die der Sonne exponierten Sektionen im Durchschnitt 1 Frassbild pro jede 2,5 bis 3,8 dm^2 Oberfläche zeigten, blieben die Eichensektionen in der Dauerbeschattung des 100 jährigen Eichenbestandes insgesamt vor dem Befall geschützt.

Durch die Untersuchung von 14 Waldlagern des Eichenholzes—fünf Lager in der Dauerbeschattung, zwei in dem Halbschatten und sieben Lager vorwiegend dem Sonnenlicht preisgegebene und sieben Holzstösse des Eichenbrennholzes wurde praktisch die Tatsache überprüft und bestätigt, dass der Eichenholzbefall durch die Bockkäfer aus der Gattung *Plagionotus* direkt mit der Besonnungszeit des Holzes proportional ist. Die schattig gelagerte Eichensektionen wurden nicht durch diese Arten in 95%, in dem Halbschatten in 40% befallen, während auf der Sonne der Anteil des unbefallenen Holzes nur 17% betrug.

Die Literaturangaben in dieser Frage sind jedoch unvollständig und lassen ausser Acht die Tatsache, dass das in der Dauerbeschattung gelagerte Holz dagegen intensiv durch dämmerungsliebende Arten befallen wird und zwar in der Regel durch den Bockkäfer *Phymatodes testaceus* L. An dem im Schatten gelagerten Holze war jedoch praktisch auf jedem Quadratdezimeter ein Gang.

Als Ergänzung zum erwähnten präventiven Schutz wird in der Literatur empfohlen auf dauerhaft der Sonne exponierten Stellen Fangscheite zum Abfangen Schädlings, der sich in wiesen jedoch durch Versuche, dass unter vollständig normalen Bedingungen die Entwicklung aller vertretenen Bockkäferarten und ihrer Parasiten ohne Störung beendet wird. Unsere Erfahrungen zeigen, dass diese Methode mit grosser Vorsicht anzuwenden ist.

Es bleibt noch übrig über einige vorläufige Ergebnisse aus der Slowakei aus der Staatsholzforschungsanstalt in Bratislava zu berichten. Die bisherigen Untersuchungen aus 50 holzbearbeitenden Betrieben zeigen, dass die Beschädigung des Holzes durch Holzschädlinge viermal grösser in den Lieferungen aus dem Walde ist (12,5%) als in den eigenen Holzlagern (2,9%).

TIME AND DISTRIBUTION OF INSECT ATTACK ON PINE AND SPRUCE LOGS

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At two localities in Sweden, pine and spruce logs were felled every ten days during spring, and inspected at regular intervals. By marking all new entrance holes in the logs at the inspections, the course of insect attack could be followed in detail.

In spring, with maximum temperatures above 12°C, *Blastophagus piniperda* L. and *B. minor* Hart. began to attack the sample logs. *Pityogenes quadridens* Hart. appeared in the middle of May, and *Ips typographus* L. and *Pityogenes chalcographus* L. began to tunnel from the end of May, when there was a large rise in temperature (maxima above 22°C).

Attacks by *B. minor* occurred until the middle of June, and by the other species until at least the end of July. After only one week from their first attack, two-thirds of the total number of *B. piniperda*, *B. minor* and *I. typographus* were tunnelling, and within one month, over nine tenths. The attack of *P. quadridens* and *P. chalcographus* followed a less rapid course, for most of these beetles had entered the logs only some time after the initial attack, *P. quadridens* only towards the middle of the swarming period. The progress of attack by these two species was apparently influenced by the weather. However, no influence of weather on the progress of attacks by the *Blastophagus* species and by *I. typographus* could be demonstrated.

Logs, which were felled during the swarming period, were immediately attacked by *B. piniperda*, *B. minor*, and *I. typographus* and after a few days by *P. chalcographus*. *P. quadridens* tunnelled into the logs only some time after felling. There is thus no safe span of time between felling and attack of the insects during swarming except for *P. quadridens*.

The distribution of attacks was influenced by a number of factors, such as the type of bark, the temperature and the condition of the inner bark.

The length of the egg tunnels of *B. piniperda* and *B. minor* was dependent on the population

density and, for the latter species, the condition of the inner bark apparently also has an influence.

The time between entrance of the parent beetles and emergence of the first young beetles was at least two months. No species had two generations, but in a few cases there was a second brood.

Conclusions. In Sweden, under normal weather conditions, the greatest number of *B. piniperda*, *B. minor* and *I. typographus* beetles tunnel at the beginning of their swarming periods. Therefore, later felled logs are less attacked. As the beetles can attack the logs immediately after felling, unbarked timber is only safe from insects when it is removed or protectively treated. Tunnelling can also occur in bad weather. Type of bark, form and duration of storage play an important role in insect attack and in the production of offspring. Logs felled in spring should be removed before the insects swarm, barked, or treated protectively.

Logs with bark, which have not been treated, should not lie in the woods more than, at the most, two months after the onset of swarming. If they have been attacked, they should be removed within two months of felling, since the emerging young beetles can endanger living trees.

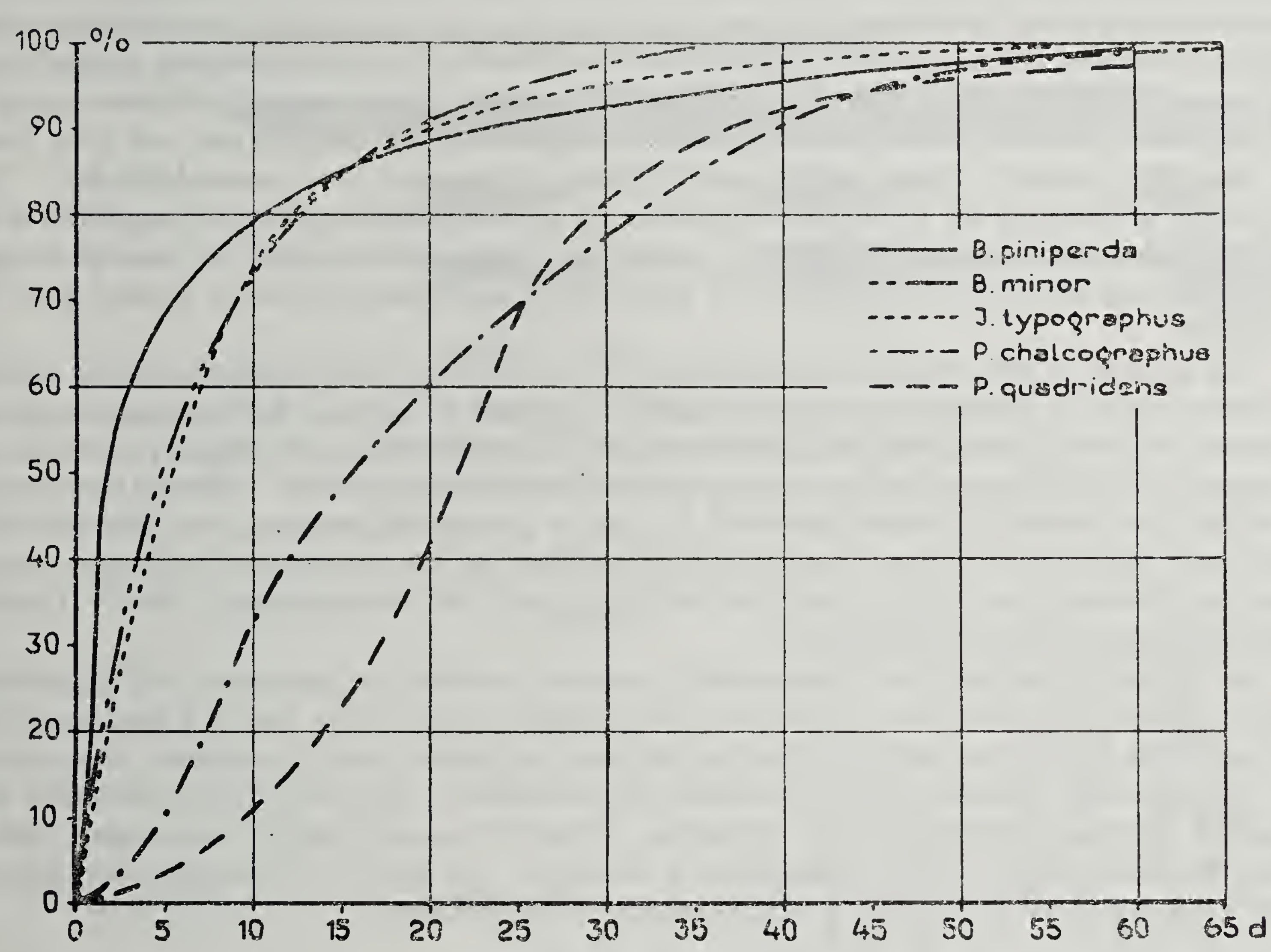

Fig. 1. The course of bark beetle attack on pine and spruce logs, from the day of the first entrance hole of the respective species, in 1963.

SOME MORTALITY FACTORS AFFECTING A POPULATION OF *SCOLYTUS SCOLYTUS* (F.) (COLEOPTERA; SCOLYTIDAE)

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A series of cut Elm logs (*Ulmus procera* Salisb.) was exposed to attack by *Scolytus scolytus* (F.) in Wytham Wood, Berks. Samples 10 cm. long were cut from these logs at intervals during the life cycle to determine the changes in the population and the causes of these changes.

The cause of death of all stages from the egg to the emerging adult could usually be determined from the traces left below the bark. Since the immature stages were confined to a small area of bark and the whole of each sample was examined, each sample could be considered as a separate population. Different logs sampled at one time had different beetle densities (100-1,000 eggs laid per 1,000 sq. cm.). Thus the effects of density on the various mortality factors could be studied.

A modification of the k-value method of Varley and Gradwell (1960, J. Anim. Ecol., 29: 399-401) has been used to examine the killing power of the different mortality factors. Due to the prolonged oviposition period and partial second generation, many stages in the life cycle may be present at one time, and the mortality factors tend to overlap in time rather than act successively; therefore, five successive stages in the development of the beetle were distinguished, within each of which the mortality factors were considered to act simultaneously on the actual number reaching the stage. The killing powers (m-values) of the mortality factors acting on each stage were calculated as the difference in the logarithms of numbers per unit area before and after their action. These m-values differ from k-values in their non-additivity. They were tested graphically for a functional response by plotting them against the logarithm of the population density on which they acted. Assuming a linear relationship, the possible density-dependence was determined statistically by testing for a significant difference in slope from the horizontal.

The total mortality was density-dependent ($P < 0{\cdot}005$) for three successive sets of samples cut before winter. Due to the increased variability, a slope of $b = 0{\cdot}5 - 0{\cdot}75$ was not significant in others cut the following year, but there seems to be considerable compensatory mortality for variations in initial density over the range of population densities studied. Plotted graphically, several of the mortality factors appeared to give a functional response, but this was only statistically significant, in more than one set of samples, for the subcortical predators, (chiefly larvae of *Medetera* spp. (Dipt. Dolichopodidae)), and the ectoparasites, (chiefly *Coeloides scolyticida* Wesm. (Hym. Braconidae)).

In the later samples, the relationship between m-value for predators and population density was clearly non-linear. With increasing density, the m-value rose to a maximum and then declined. This was probably due to predator satiation, since the density of predators was approximately constant above a medium beetle density. Mortality due to parasites only showed a functional response above a certain threshold density slightly lower than that at which the killing power of the predators was maximal. At high host densities, the parasites partly compensate for the decline in killing power of the predators.

ASPECTS OF THE LIFE HISTORY OF THE AMBROSIA BEETLE *PLATYPUS CYLINDRUS* FAB.

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Platypus cylindrus is the only platypodid ambrosia beetle occurring in Britain. During July to September beetles fly to attack oak logs and stumps in which they bore galleries. Eggs are laid from 3 weeks after a tunnel is started and under the most favourable circumstances the

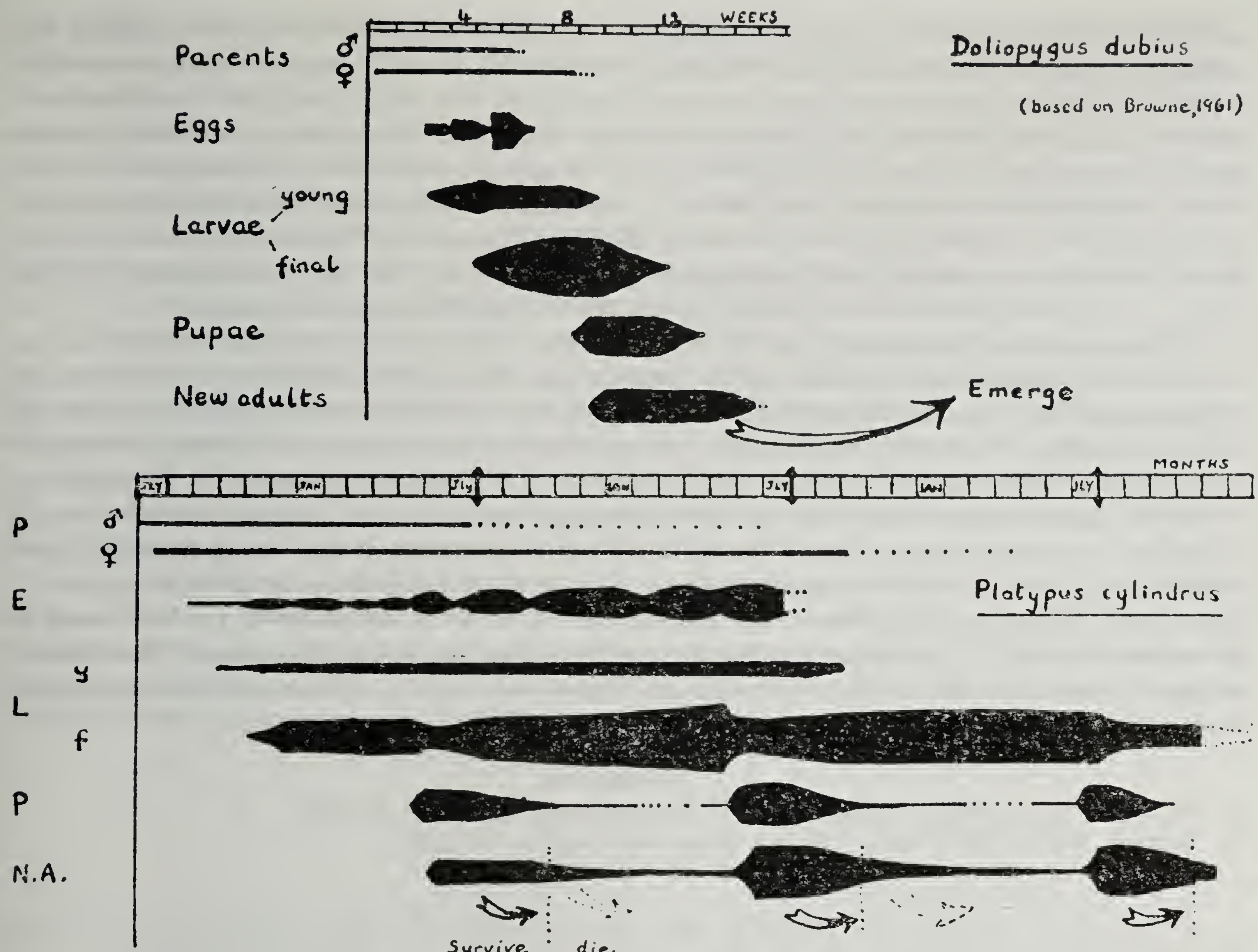

FIG. 1. Schematic life histories of *Doliopygus dubius* and *Platypus cylindrus*.

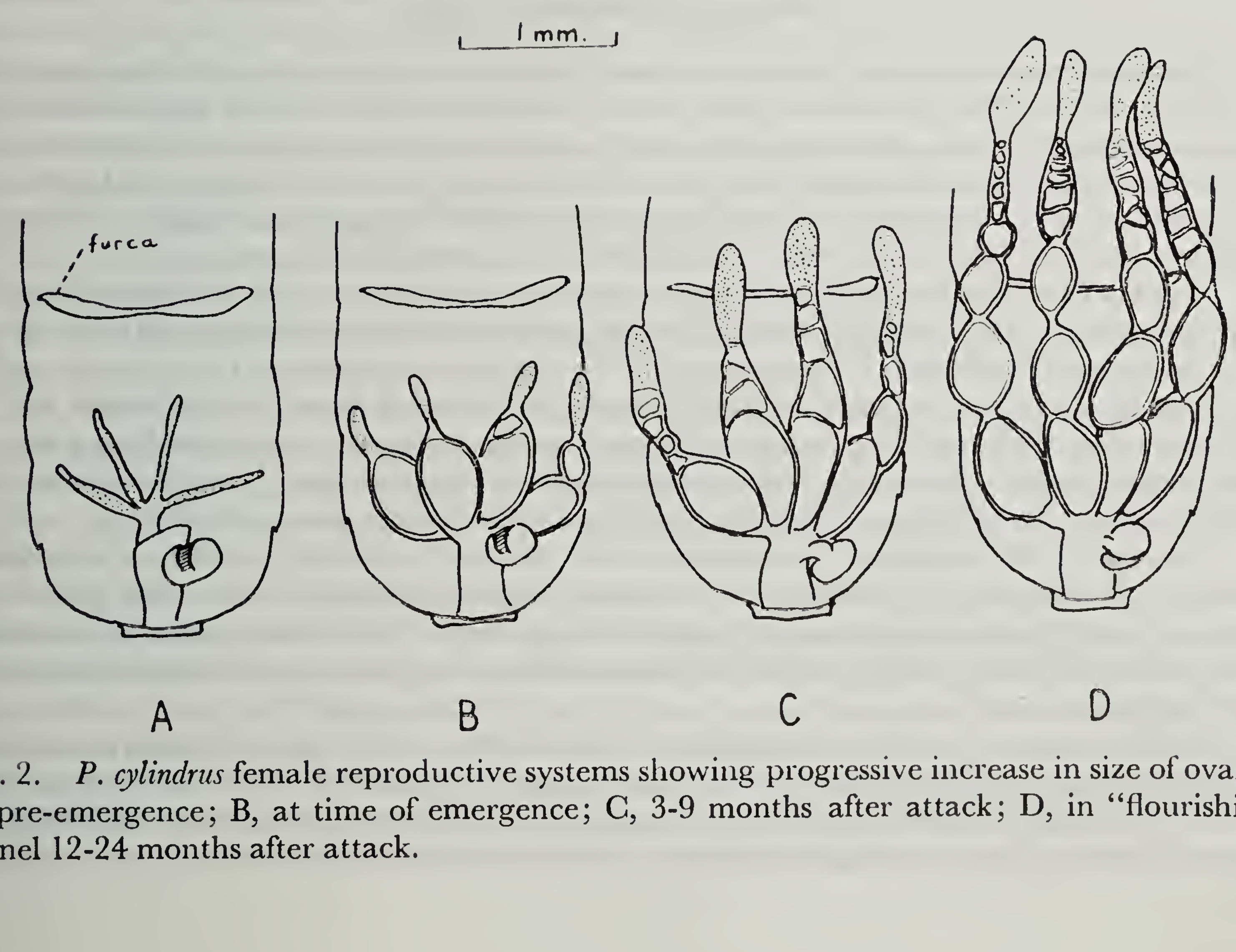

FIG. 2. *P. cylindrus* female reproductive systems showing progressive increase in size of ovaries; A, pre-emergence; B, at time of emergence; C, 3-9 months after attack; D, in "flourishing" tunnel 12-24 months after attack.

new generation of beetles emerges the following summer. The parent female continues egg-laying throughout the year and the resulting beetles reach the adult stage too late for the flight period. They emerge sporadically however throughout the winter and die. As the female can lay eggs intermittently for 2-3 years in suitable logs, effective emergence can take place in successive summers for 3 or 4 years after attack. It is suggested that *P. cylindrus* does not have an intrinsically seasonal cycle but instead a continuous cycle resembling that of a tropical platypodid such as *Doliopygus dubius* (Browne, 1961). The cycle in *P. cylindrus* is longer and has, superimposed on it, an effective emergence period governed by the temperature for flight (fig. 1). This would accord with Schedl's view that *P. cylindrus* is a relict species.

The egg-laying capacity of the female increases as the gallery lengthens and is accompanied by a gradual enlargement of the ovaries (fig. 2). At the final stage, at least a year after attack, there may be 40 or more developing oocytes though not more than 8-12 are ripe simultaneously. Marked lengthening of the gallery system occurs only when the female's excavation is augmented by that of last instar larvae: the colony then enters a "flourishing" condition and produces a hundred or more emerging beetles in the 2nd summer after attack. However, in many instances larval boring is slight, the increase in egg laying capacity is not marked and there are few emerging beetles. The factors which allow the flourishing state to develop are not known but presumably include climate and the suitability of the host wood for the ambrosia fungi. Particularly suitable conditions leading to the widespread "flourishing" of tunnels may account for the outbreaks of *P. cylindrus* attack on an economically important scale which occur in certain years only.

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EVALUATION OF OUTBREAK POPULATIONS OF THE JACK-PINE BUDWORM, *CHORISTONEURA PINUS* FREEMAN (LEPIDOPTERA)

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The jack-pine budworm, *Choristoneura pinus* Freeman, has erupted to outbreak proportions periodically in the *Pinus banksiana* Lamb. forests of central North America since its biological characterization in 1925. Although defoliation often is extensive, mortality of merchantable trees may rise no higher than one per cent. Mortality of reproduction and small saplings in the understory and in openings, though, frequently reaches 30 per cent or higher. When the budworm reaches high levels, however, widespread tree mortality may occur.

In order to predict impending budworm outbreaks, their extent and the expected severity of the defoliation, it is necessary to evaluate the insect population sufficiently early to permit the development of emergency controls should the situation require it.

Pole pruners were employed to clip 15-inch foliated twigs from the mid crown and the egg, overwintering larval, late larval and pupal populations were determined on a time or linear foliage basis. These population estimates were related to each other in sequence and then to estimated defoliation. Coefficient of Correlation analysis was employed.

Although a few significant correlations were obtained between population densities of successive life stages, no consistent relationships could be detected between the population density of any life stage and resulting defoliation intensity. Inclusion of data on parasitism of the various life stages and previous defoliation failed to improve the statistical soundness of the relationship.

In 1957, when the most recent eruption of the budworm reached its peak, light to moderate defoliation was evident over several hundred thousands of acres of *P. banksiana* forest in northwestern Wisconsin. Population surveys for eggs indicated that approximately 200,000 acres were sufficiently infested to require emergency control the following season to prevent extensive

tree killing. Collection of overwintering larvae on small branches substantiated the previous survey and plans were made by forestry officials to activate an emergency abatement program.

Because of the afore mentioned lack of a consistent significant relationship between population density of successive life stages and defoliation, the final decision to apply chemical control was delayed until larval development reached the 4th instar. For it is in the 4th and successive instars that most feeding occurs. In the interim, budworm population levels at which emergency treatment was to be initiated were set at: (*a*) overwintering larvae, 10 newly emerged larvae per 30 terminal buds or staminate flower clusters, and (*b*) 4th instar larvae, 3 larvae per 15 inches of foliated twigs.

Dissection of overwintering budworm larvae collected during late winter suggested a high rate of parasitization by *Apanteles fumiferanae* Vier. Because of the variability in the degree of attack it was not possible to predict precisely the magnitude of the reduction in the bud-worm population this parasite would cause. Also, it was made additionally difficult by the delay of the parasite emergence from the budworm until its host reached the 4th instar. The emergency control program was activated, insecticide was purchased, aircraft were employed, and spraying began on the most severely infested areas.

After *A. fumiferanae* kills the budworm larva, it emerges from its host and spins a white cocoon nearby. Such large numbers of these white cocoons began appearing that it was evident a revaluation of the forest scheduled for treatment was required. This re-examination was conducted immediately and it was possible to reduce the size of the treatment area from 200,000 acres to approximately 30,000 acres or 85%.

SUR L'INCIDENCE DE LA TORDEUSE DU CHENE (*TORTRIX VIRIDANA* L.) (LEPIDOPTERA) DANS LA REPUBLIQUE POPULAIRE ROUMAINE

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Tortrix viridana est un important ravageur des forêts de chêne de la Republique Populaire Roumaine. La prévision des invasions de cet insecte a à la base la prospection des fléaux et l'éstimation de l'intensité des invasions. Ces activités constituent une technique toujours difficile et pas constament satisfaisante. Les auteurs sont d'avis que pour l'ameliorer il faudrait tenir compte aussi des facteurs du climat.

Les auteurs ont cherché la relation entre l'extension des surfaces des forêts infestées dans les 16 regions administratives du pays, et le climat- à savoir la température et les pluies des mois d'avril, de mai et de juin- de 1950 à 1963.

Les résultats ont été les suivants:

1. De 1950 à 1963 on a signalé des invasions dans 14 régions du pays.
2. Les attaques ont été plus faibles dans les régions nordiques et plus puissantes dans les régions du sud et de l'est du pays.
3. Les superficies attaquées d'une région pendant les 14 années constituent des succesions des surfaces presentant des acroissements et des décroissements. L'éxistence d'une succesion des maxima et des minima, met en evidence le fait que les invasions d'une région ont presque la même phase de l'évolution, ce qui montre l'influence du climat sur le developpement de l'insecte.
4. La poursuite concomitente de la marche des invasions et de l'évolution des données climatiques a mis en évidence la liaison qui existe entre les minima des invasions et les minima des temperatures et les maxima des hauteurs des pluies d'une région. En 1955 on a observé un minimum des superficies dans tout le pays. Deux autres minima se sont succédé, dans des differentes régions: un de 1957 à 1959 et un autre de 1960 á 1962. Simultanément à ces minima on a observé des minima de la temperature (1°-2° sous la moyenne plurianuelle de la région) et des maxima pluviometriques (plus de 20% au dessus de la moyenne.)
5. On a constaté aussi que les effets des temperature et des pluies sont d'autant plus

grands, que ces facteurs ont la tendence d'exercer leurs influences deux, trois ou quatre années dans le même sens et sans interruption.

6. On peut expliquer la présence de *Tortrix viridana* dans toutes les régions par la temperature moyenne du moi d'avril qui est de 8°-11° et par la temperature d'éclosion des larves qui est de 9°.

7. On explique les invasions faibles ou leurs absence dans le nord du pays, ou dans quellques années, partout dans le pays par les temperatures inférieures à 9° au mois d'avril.

8. Les données météorologiques peuvent être utilisé pour la prevision de la tendance des invasions, mais il faut que la prévision soit faite pour des régions moins grandes et avec des climats presque uniformes.

ECOLOGICAL STUDIES OF THE NANTUCKET PINE TIP MOTH (*RHYACONIA FRUSTRANA* COMST.)

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Preliminary publications on this tip moth (2) discussed the host habits and damage caused and raised the question of possible effects on it of changing silvicultural practices. Since then, there have been changes, some of which directly influence the severity of attack. During the intervening years 1928-64, various programs sponsored the planting of large acreages of even age trees, in the early phases often on poor sites, but in recent years on former crop or pasture land.

It has been reported that damage was related to poor site selection or thin soils. While this is true, our studies show that heavy damage on poor sites is not a result of the site *per se*, but a response of the moth to decreased vegetative competition usually characteristic of such areas. Wakeley pointed out that damage was most severe in pure, even age stands with no overhead shade and little vegetative brush. Foil, *et al.* (1) and myself have observed that naturally reseeded stands under a crown canopy suffer relatively light damage.

The diversion of fields from row crops to artificially planted, even age stands of young pine resulted in an increase in the intensity of tip moth infestation and resultant damage. Damage was most spectacular in the second and third year of growth and sometimes extended through the fourth and fifth growing seasons, occasionally longer. In many instances damage in old field stands was quite severe while nearby natural stands under a canopy would be lightly or not at all infested. Naturally occurring reproduction in old fields often was damaged, usually less so than artificial plantings.

To test the relationship of vegetative cover to tip moth infestation, an experiment was designed which included cultivation and noncultivation, with both loblolly pine (*Pinus taeda*) and shortleaf pine (*Pinus echinata*) as hosts.

In 1962, a field of well-drained Costal Plain type soil was fallowed to equalize soil and growth conditions. In the spring of 1963, two blocks of approximately three acres each, were planted to pine, one block to loblolly the other to short-leaf pine. One-half of each block was cultivated, the other was left alone for competitive vegetation to develop freely. Within each sub-block, a total of 250 trees in 10 plots were established as test trees. These test trees provided the data for height growth and gross infestation counts. Fifty trees, five in each plot, provided for measuring the degree of attack.

In 1963, no control measures were applied and by mid-August infestations were active in all cultivated trees.

Infestation counts were made, October 1, 1963, and June 9, 1964. The data thus reported would span the activity of at least four generations of tip moth.

The results of the test are as follows:

TABLE 1.
Effect of cultivation and competitive vegetations on Nantucket pine tip infestations in short-leaf pine. Arkansas, U.S.A., 1963-64.

Species and Treatment	*Av. ht.* (*ft.*) *Oct.* 1963	% *trees Infested* (250)		% *tips infested* (50 *trees*)	
		Oct. 1963	*June 1964*	*Oct. 1963*	*June 1964*
Short-leaf pine *Pinus echinata*					
Cultivated	1·5	96·9	93·4	36·0	47·8
Non-cultivated	1·3	3·3	26·8	1·6	2·8

Attention is called to the slight difference in tree height between the cultivated and non-cultivated trees at the end of the first growing season. A great difference existed between the number of infested trees and percentage of tips infested in the two treatments.

A similar pattern of infestation was evident in the loblolly pine plots. The tabular summary illustrates these differences.

TABLE 2.
Effect of cultivation and competitive vegetation on Nantucket pine tip moth infestations in loblolly pine. Arkansas, U.S.A., 1963-64.

Species and Treatment	*Av. ht.* (*ft.*) *Oct.* 1963	% *trees Infested* (250)		% *tips infested* (50)	
		Oct. 1963	*June 1964*	*Oct. 1963*	*June 1964*
Loblolly pine *Pinus taeda*					
Cultivated	1·5	99·0	87·9	78·7	77·6
Non-cultivated	1·3	7·7	52·2	1·8	1·4

Thus the evidence clearly indicates that vegetative competition retards the development of tip moth infestations, whereas trees openly exposed to free flight of the tip moth adults may be heavily infested. Since plantings in old fields often are relatively free of vegetative competition and new plantings in such fields often grow off fast under otherwise favorable conditions, tip moth infestations have become of greater importance in artificially planted even age stands in such fields.

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PROBLEMS OF GALL MIDGES ATTACKING CONIFEROUS TREES IN JAPAN

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Before 1950 very little was known of gall midges attacking coniferous trees in Japan. Following systematic collections, studies have been started to obtain more exact estimates of the damage caused by these insects as well as more information on their biology and ecology, aimed towards the development of appropriate control measures.

Sugi Tree Pests. The two most prevalent midges found on infesting Sugi tree were the Sugi Trunk Midge, *Thomasiniana odai* Inouye and the Sugi Needle Midge, *Contarinia inoyei* Mani.

The Sugi Trunk Midge has been found by the writer in Japan in 1953. The pink larvae live solitarily or in clusters under the bark of the Sugi tree. The damage done is caused by the larvae tunnelling up and down the bark of the trunk in the subcortical layer or cambium. The bark at the infested areas flaked off easily, revealing clusters of grown larvae.

The epidemic, which started in 1954, reached a peak in 1959 when damage to 3,558 hectares and 1,036,490 trees was recorded. (Table 1).

In 1958 Oda concluded that dusting twice with 3% gamma BHC dust 60 kg. per hectare gave satisfactory results against this pest.

The Sugi Needle Midge has been known as a serious pest of Sugi trees in Japan since 1937. However, there were no epidemic infestations of this pest until 1951.

In 1955, the trend turned sharply upward and damage to 113,361 hectares and 193,839,279 trees was recorded. As shown in Table 1, severe infestations have continued from 1955 to the present.

Insufficiency of shoots to produce the cuttings of Sugi trees, the decline of the plant percentage of rooted cuttings and unsuccessful results in young plantations of the Sugi trees are caused by the attack of this midge.

Hitherto, many entomologists believed that all larvae of this insect hibernate in the soil during the winter, and that it has only one generation per year. So they usually conducted their dusting once a year with 1% gamma BHC in spring. But recently the writer has found that certain of them pass the winter in the gall of Sugi needles, and drop to the ground in early spring, and that they have two or more generations per year. (fig. 1).

Therefore, the forest owner should realize that dusting twice or more with 1% gamma BHC dust at 2 or 3 months interval may be recommended in future.

Pine Tree Pest. The Japanese Pine Needle Gall Midge forms the gall at the base of needles of *Pinus densiflora* and *Pinus thunbergii* in Japan and Korea. The midge was previously considered by many entomologists to be *Thecodiplosis brachyntera* Schwargrichen which is widely distributed in Europe.

In 1955, the writer described this fly as a new species under the name of *Thecodiplosis japonensis* Uchida et Inouye (1955 and 1964).

This midge has been known as a serious pest of Japanese pines since 1914 in Japan. The epidemic, which turned upward in 1950, reached a peak in 1962 when damage was recorded to 4,519 hectares and 12,876,000 trees. (Table 1).

As the result of an attack the needles usually become yellow and drop to the ground in the winter season. The infested needles usually become short and with a gall at the base, but often some needles bend over.

According to Takagi (1955), 0·5-1·5% Folidol dust and 30-50% Nitrolime were more effective against the larvae than 10% DDT dust and 3% gamma BHC dust. So lately it has been recommended that 1% gamma BHC dust, 30 kg. per hectare be used against adult flies in the spring—and 3% BHC dust and Nitrolime dust mixture be used against larvae in autumn because Folidol dust is dangerous to both men and beast.

Control of this pest may be achieved by combining the application of effective insecticides with rational forest treatment; especially cutting heavily infested large trees from the forest, and burning the branches and needles in summer.

Table 1. DAMAGE BY GALL MIDGES ATTACKING CONIFEROUS TREES IN JAPAN

Midge names	Sugi Trunk Midge		Sugi Needle Midge		Japanese Pine Needle Gall Midge	
Fiscal year \ Damage	Area (ha.)	Trees	Area (ha.)	Trees	Area (ha.)	Trees
1950	0	0	0	0	2,757	4,703,536
1951	0	0	188	249,500	9,002	3,047,850
1952	0	0	5,158	6,512,000	2,767	-
1953	0	0	11,896	18,713,000	2,394	-
1954	560	472,587	38,099	53,760,220	711	16,699
1955	1,453	1,404,312	113,361	193,839,279	1,165	892,000
1956	1,285	1,055,562	110,751	223,021,726	1,329	260,340
1957	81	149,500	87,188	190,950,894	840	1,092,588
1958	766	836,779	103,769	208,205,734	1,098	801,800
1959	3,558	1,036,490	94,557	218,671,506	1,490	1,580,630
1960	3,727	16,740	86,975	196,000,707	3,387	5,059,132
1961	3,719	371,000	90,305	218,478,000	2,979	5,623,000
1962	46	63,000	80,072	217,437,000	4,519	12,876,000
Average	1,688	600,663	68,527	145,486,639	2,649	3,268,507

SOURCE: JAPANESE FORESTRY AGENCY

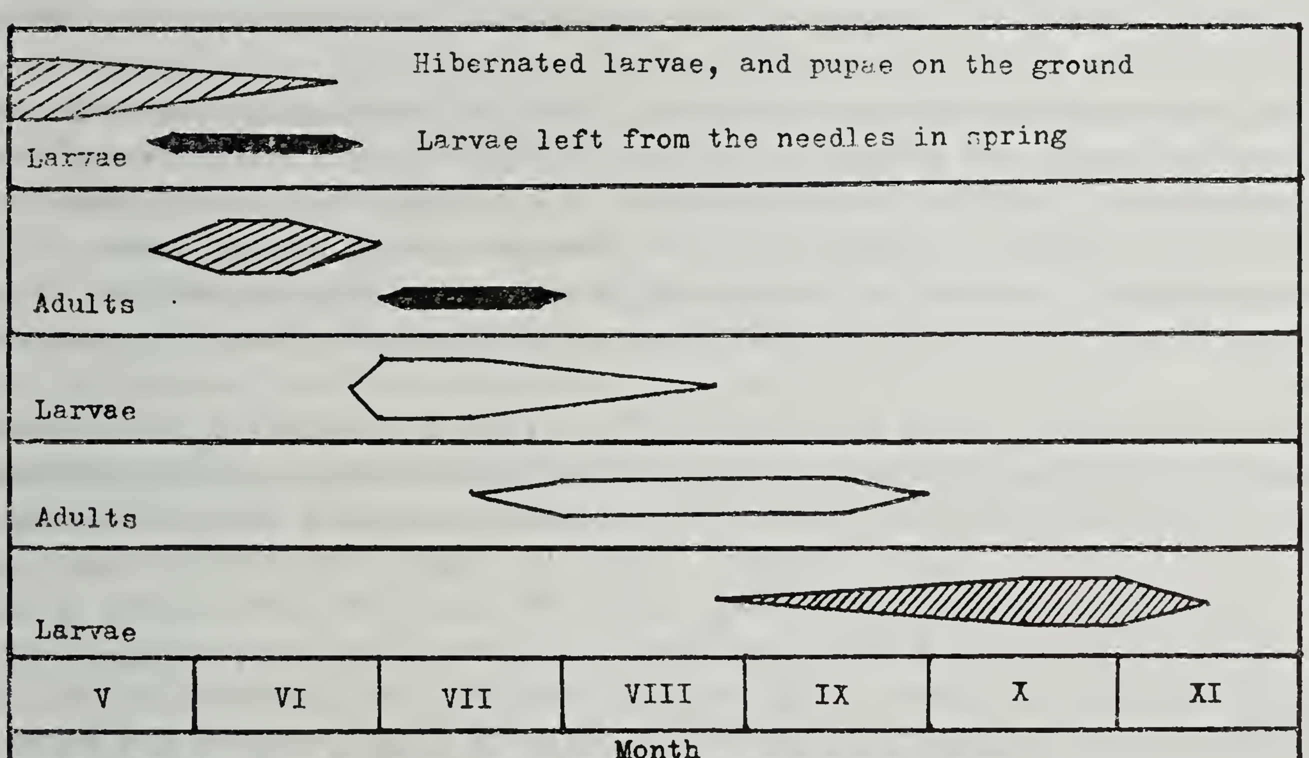

Fig. 1. Chart showing occurrence of larvae, pupae and adults of *Contarinia inouyei* Mani throughout the year in the southern part of Hokkaido, based on earliest and latest records.

DYNAMICS OF *BISTON HISPIDARIA* AND *PHIGALIA PEDARIA* POPULATION IN OAK-WOODS OF THE STEPPE ZONE OF THE U.S.S.R.

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The outbreak of mass reproduction of *Biston hispidaria* and *Phigalia pedaria* loopermoths in oak woods of the steppe zone of the European part of the U.S.S.R. lasted from 1957 to 1962. Studies of the dynamics of the moth population were carried out in the woods of the Khoper reservation in the Voronezh district which contains middle-age flood-plain oak and elm of 2nd-3rd quality.

During the first two years the population of the moths was at a low level but from 1959 it began to increase rapidly and reached its maximum in 1961.

The primary nidi of moth reproduction appeared in flood-plain grassy oak woods. From the biocenotic point of view this is the simplest and unstable type of the forest. Then the nidi spread to elm-and-grass, lily-of-the-valley and blackberry oak woods. The spreading of the nidi was due to active movement of caterpillars which indulge in frequent migrations, usually moving for pupation from heavily damaged woods to intact or little damaged ones. During 3 years (1959 to 1961) the area of the nidi expanded 4 times and the population of the moths increased 5 times. In the autumn of 1960 the average pooulation of caterpillars per square metre was 29·6. The population of the moths reached its maximum in 1961, when the stock of caterpillars of the IIIrd-IVth stages was 85·7 per 100 leaves. In the nidi the caterpillars ate the foliage completely and suffered from shortage of food.

The reproductive capacity of the moths changed only by 10-22% during the years of the outbreak.

The rapid increase of the population was promoted by two-year coincidenee of the open-bud phase of the early forms of oak and elm with hatching of caterpillars which prefer these species. Experiments to study food specialization of the moths have shown that the minimal mortality of caterpillars was observed when they fed on the leaves of oak and elm. In cases of food shortage they fed on almost all arboreal and herbaceous species. In this ease their reproductive capacity markedly decreased and the mortality increased.

As a result of successive registration of the mortality of eggs, caterpillars, pupae and adults a "Survival table" was composed and a population mortality curve for 1960 and 1961 was plotted.

In the period of the outbreak culmination (1960-1961) the leading role in decreasing the population of the moths was played by *Calosoma inquisitor* L. of which the number increased 2 to 2.5 times a year. In 1960 they destroyed from 5·5 to 26·5 per cent of all pupae in the areas examined. We also found 9 species of endoparasites on eaterpillars and pupae.

The total mortality caused by parasites and predators in 1960 and 1961 was 19·6 and 48·5 per cent respectively, showing that they did not control the population, nor cause the outbreak to subside.

Nuclear polyhedrosis which developed swiftly in 1961 appeared to be the decisive factor in the dynamics of the population in the peak period of the outbreak. At first the mass of sick caterpillars could be found on the borders of and in thin woods but then the disease spread to the depth of the forest as well. During 11 days the moth population became practically extinct. The number of dead caterpillars which fell from the trees during 8 days of the disease was 457·4 (for *Phigalia pedaria*) and 184·9 (for *Biston hispidaria*) per square meter of soil surface under the crowns of trees. The maximal mortality was observed on the 3rd-4th day of the epizootic when the number of dead caterpillars of *Phigalia pedaria* and *Biston hispidaria* per square meter was 340 and 142·8 respectively. The development of polyhedrosis was promoted by weather conditions of 1960 and 1961.

RECENT INVESTIGATIONS ON GALL BUG (*PHYTOLYMA* SP.) INJURY TO THE IROKO TREE (*CHLOROPHORA* SPP.)

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Chlorophora excelsa and *C. regia* extend across the width of tropical Africa. Both are found in Liberia, Ivory Coast, Ghana and Togoland but elsewhere these species have distinct distributions. The timber is valuable for decorative and structural purposes and has a high resistance to insect attack and fungal decay. The trees are, however, frequently attacked by a Psyllid gall bug. The holotype described from Sierra Leone by Walker in 1852 was named *Psylla lata* but was subsequently reclassified as *Phytolyma lata*. *Phytolyma* appears to be confined to *Chlorophora*. The eggs laid on young tissues hatch in about eight days; the first instar nymphs crawl over the surface and probe into the tissues. The resultant plant stimulation produces a gall enclosing the insect. Passing through five instars, development into an adult is completed within fourteen days. The gall opens releasing the bug which, after mating, oviposits and initiates a new life cycle. Rapid increase in the population results in the production of a mass of galls. All young trees in a nursery may be killed and *Phytolyma* damage is the most important factor in preventing establishment of new plantations. Mature trees are not seriously affected but their young growth supports a sufficient *Phytolyma* population to form a reservoir of infestation throughout the year. Owing to the wide distribution of *Chlorophora*, and the readiness with which the stumps coppice, plantation of young trees in *Phytolyma*-free areas is impracticable. More than one species or variety of *Phytolyma* may be involved since *C. regia*, when grown in Nigeria, is resistant to attack although susceptible in Sierra Leone. Pending clarification of the systematics of *Phytolyma* it is wise to restrict the name *P. lata* to the insect attacking *C. regia* in Sierra Leone.

Since parasitization (which may be heavy amongst the nymphs) provides insufficient control, artificial methods have been sought. Contact insecticides are inapplicable for several reasons, including the rate of plant growth which would necessitate repeated treatments to prevent attack on young trees. The systemic insecticides Phorate and Dimethoate applied in granular form (which has several advantages) have been tested. Phorate proved unsuitable for curative purposes but showed more promise for the protection of seedlings and young trees. Dimethoate has not been fully evaluated for protective purposes. Since the most serious result of *Phytolyma* attack is the decay and die-back following bursting of the galls, the systemic fungicides (Phytoactin and Actidione) were tested for protection against secondary infections. The former proved ineffective and the latter produced marked phytoxic effects.

Experiments to simulate attack by continuous removal of young shoots over a period indicated no loss of plant vigour, suggesting that *Phytolyma* might affect growth-regulating mechanisms. Chromatogram studies by Wright of Wye College have indicated the presence of two auxins in the gall tissues apparently absent from healthy *Chlorophora* leaves. Further analyses of nymphs and adults indicated they contained and may secrete these two auxins and their identification is now being attempted.

Future lines of research indicated are methods of physiological interference with gall development and further insecticidal tests.

AN EXPERIMENT IN BIOLOGICAL CONTROL OF THE BALSAM WOOLLY APHID IN NORTHWESTERN UNITED STATES

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In 1957, a program of importing and colonizing insect predators was undertaken to control the balsam woolly aphid (*Chermes piceae* Ratz.) in the northwestern United States. This European insect has become widely distributed in the forests of Oregon and Washington

where it now is a serious enemy of *Abies lasiocarpa* (Hook.) Nutt., *A. amabilis* (Dougl.) Forbes, and *A. grandis* (Dougl.) Lindl. Many native predators attack the aphid but are ineffective in controlling it.

So far, 22 species of insect predators have been imported from India, Pakistan, Japan, Australia, Sweden, Germany, and Czechoslovakia. Cooperators in the program have been the Canada Departments of Forestry and Agriculture, laboratories of the United States Department of Agriculture at Paris, France, and Moorestown, New Jersey, and laboratories of the Commonwealth Institute of Biological Control at Delemont, Switzerland, Bangalore, India, and Rawalpindi, Pakistan.

Five of the introduced predator species have become established. A sixth produced progeny and then disappeared. None of the remaining predators produced progeny, and most failed to survive even a few weeks.

The established species are *Laricobius erichsonii* Rosen. (Derodontidae), *Pullus impexus* Muls. (Coccinellidae), *Aphidoletes thompsoni* Mohn (Itonididae), *Cremifania nigrocellulata* Cz. (Chamaemyiidae), and *Leucopis obscura* (Hal.) (Chamaemyiidae). All were imported from Europe. None of the Asian or Australian predators survived.

Laricobius erichsonii and *Aphidoletes thompsoni* appear to be the most effective introduced predators. Both develop large populations and have moderately good rates of dispersal. They are compatible for liberation in the same areas: *L. erichsonii* attacks early in the season and concentrates on the moderately heavy to heavy aphid populations; *A. thompsoni* attacks about mid season and feeds on light to heavy populations. To date, the other three established species have shown little promise of being effective control agents.

In spite of the sizeable populations attained by some of the predators in their new environment, control benefits in northwestern United States are not encouraging. In one forest stand, where four of the introduced predators have been established 4 to 5 years, accumulated tree mortality since the first release is 55 per cent. Similar conditions prevail in other stands. Hence, it appears unlikely that current tree killing will be alleviated by predators introduced to date.

However, biological control can possibly be successfully integrated with forest management practices. In the over-age, unmanaged forests of the present, thousands of trees may be infested simultaneously. Under these conditions, it probably is unreasonable to expect predators to prevent tree-killing. The managed forests of the future will be generally young and of mixed age classes, where trees will be infested only as they grow into susceptible age, allowing the predators to concentrate their efforts. Furthermore, investigation of predators is continuing in Asia and elsewhere; it is possible that more effective species will be found. In short, the future holds promise.

INVESTIGATIONS INTO THE NATURAL ENEMIES OF *SIREX* IN EUROPE

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The accidental establishment of *Sirex noctilio* in Australia led to the formation in 1963 of the Sirex Biological Control Unit, for the purpose of investigating in Europe the ecology of siricids in coniferous trees, especially in relation to the importance of natural enemies in the control of these insects.

When the Unit was formed, it seemed that few parasites might be encountered apart from *Rhyssa persuasoria* and *Ibalia leucospoides* which were the subject of study by Chrystal and by Hanson a generation ago. However, it was considered that geographical races of these wide-ranging species might exist, and it was thought desirable to obtain material of them from parts of Europe closer climatically to the Australian areas concerned.

During the past year Dr. J. P. Spradbery, an officer of the Unit, has made two extensive surveys through West Germany, Switzerland, France, Jugoslavia, Spain and Portugal, and

infested logs from nearly forty points in western and central Europe have been assembled at the Unit for study. Future surveys will extend into Scandinavia, central and eastern Europe, and possibly further afield.

Already, the investigation has changed substantially our original picture of the parasite complex of the coniferous siricids. In place of the original two, so far we have seven parasites of interest, and it is almost certain that others will be encountered.

In the genus *Rhyssa* there is the wide-ranging *persuasoria*, the central and eastern European species *amoena*, and we expect to find *lineolata* Kriechbaumer in central Europe. In the genus *Megarhyssa* we have obtained *emarginatoria* from Switzerland and France, and may expect to discover *superba* and probably other species attacking siricids. Of parasites of the genus *Ibalia* we have at least two species—*leucospoides* and *drewseni*—and it is quite possible that others occur. *Coleocentrus* is a European genus containing three or four species that may be parasites of siricids. So far we have found only *Coleocentrus excitator* in Switzerland. An interesting parasite encountered is *Pseudorhyssa ruficoxis*, a hyperparasite on *Rhyssa persuasoria* Many other parasite species have been obtained (such as species of *Ephialtes*) but these are less likely to be parasites of siricids. It is hoped to clarify the host relationships of these species.

It is clear that the parasites associated with coniferous siricids in Europe are diverse, and probably have markedly different climatic needs, and it seems likely that these parasites will differ in ecological suitability for the Australian environment. The species that the Unit has so far sent to Australia include *Rhyssa persuasoria*, *Megarhyssa emarginatoria*, *Ibalia leucospoides*, and *Ibalia drewseni*, strains of these species from different geographic areas being provided separately. No difficulty has been experienced in getting these species to Australia without significant mortality.

Generally in Europe infestation of coniferous trees by siricids is at a low level, seldom causing economic loss. Healthy trees are attacked infrequently, if ever, but many factors adversely affecting the trees may make them subject to infestation. That damaged trees do not inevitably become infested may be the result of low population density of the siricids, and parasites may play an important role in maintaining this low density.

RESEARCH ON *SIREX NOCTILIO* IN AUSTRALIA, WITH PARTICULAR REFERENCE TO BIOLOGICAL CONTROL

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Sirex noctilio was first discovered during the summer of 1951-52 near Hobart, Tasmania, in a small commercial plantation of *Pinus radiata*. An attempt to eradicate it from this forest was unsuccessful and within a few years it was known to have spread through the centre of the island almost to the north coast. It is not yet established in any of the important plantations in the north of Tasmania. The Tasmanian Department of Agriculture introduced the larval parasite *Rhyssa persuasoria* in 1957, and the egg parasite *Ibalia leucospoides* in 1960, both from New Zealand. In late 1961 *S. noctilio* was discovered near Melbourne, Victoria, and it is now known to be present over a large area of south eastern Victoria. A large scale attempt is being made to eradicate it from this area.

Research on *Sirex* is being carried out by three organisations:—

1. Division of Entomology, C.S.I.R.O.—biological control, embracing the introduction of parasites from many parts of the world, and evaluation of the two established parasite species; and detailed studies of the biology and ecology of the host and its parasites.

2. Forest Research Institute (Commonwealth Forestry and Timber Bureau)—tree physiology in relation to *Sirex* attack; tree resistance; relationships between the host tree and the fungal symbiont of *Sirex;* and the effects of thinning, pruning and fertilizing on tree resistance to *Sirex* attack.

3. Waite Agricultural Research Institute, University of Adelaide—*Sirex*—fungus relationships; and the possible use of insecticides in *Sirex* control.

There is abundant evidence that *Sirex* has been the primary cause of tree mortality in the plantation near Hobart, just as it has in New Zealand. It is feared that similar mortality will occur in some important plantations on the mainland if *Sirex* spreads to them, particularly in South Australia where the summer is hot and dry.

Since the research programme began in 1962 *Rhyssa lineolata* has been introduced from New Zealand; *R. persuasoria* var. *himalayensis* from the Himalayan region; *R. persuasoria* from England and Europe; *Ibalia leucospoides* from England; *I. ensiger* from California; and other species of *Rhyssa*, *Megarhyssa* and *Ibalia* are being received at the present time from Europe and North America. Only the first two species mentioned have been released in the field so far.

Early results of sampling in the forest and surrounding areas suggest that the combined effect of *R. persuasoria* and *I. leucospoides* is no more than a 15 per cent reduction of the *Sirex* population, and that *Ibalia* is responsible for the major part of this reduction. Parasitism was much higher (30 per cent) in 10 year old regeneration. *Rhyssa* has not been recovered outside the forest in which it was liberated but *Ibalia* has dispersed to a distance of at least 40 miles.

ANOBIIDES RAVAGEURS EN ESPAGNE DES BOIS MIS EN OEUVRE

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Les anobiides qui peuvent envahir en Espagne le bois sec mis en oeuvre se partagent dans huit genres: *Xestobium*, *Ernobius*, *Anobium*, *Oligomerus*, *Nicobium*, *Stegobium*, *Ptilinus* et *Eutheca*.

La "Grande vrillette" *Xestobium rufovillosum* Deg., très rare en Espagne, n'est connue que du nord du pays, ses attaques, plutôt sporadiques, sont de faible intérêt économique.

Ernobius mollis L. se rencontre ça et là dans toute la péninsule sous les écorces des pins morts sur pied; bien plus rarement dans les entrepôts du bois; ses attaques sont toujours conditionnés par la présence de l'écorce necessaire pour le développement de la larve.

Parmi les *Anobium* il n'y a que *punctatum* Deg., très fréquent partout, et *carpetanum* Heyd., observé dans le centre, mais aussi dans le sud et le nord du pays, qui s'avérent très nuisibles au bois ouvré à l'intérieur des appartements. *A. pertinax* L., connu seulement des Pyrénées centrales où il est, d'ailleurs, fort rare, bien que susceptible d'être trouvé dans le bois de construction, il est bien moins dangereux que *punctatum* et *carpetanum*.

Oligomerus ptilinoides Woll. est un élement méditerranéen très abondant dans le levant espagnol et l'Andalousie, plus rare dans le reste du pays. On le rencontre dans les meubles à l'intérieur des habitations et les destructions qu'il occasionne aux pieds de chaises, tables, armoires, etc. sont très importantes.

Nicobium castaneum Ol. à large répartition ibérique demeure essentiellement ennemi des vieux livres; néanmoins il peut se développer (notamment la var. *hirtum* Ill.) dans le bois mis en oeuvre, auquel il ne cause, en réalité, que fort peu de dégâts. Quant à *N. villosum* Brull., l'un des élements atlantiques, il n'habite que l'extrème SW de l'Espagne et ses dommages sont bien plus faibles encore que ceux du *castaneum*.

La "Vrillette du pain" *Stegobium paniceum* L. très commune partout, est un redoutable ennemi de toute sorte de produits entreposés, mais elle n'est jamais observée, chez nous, dans le bois travaillé et ne saurait y commettre de dommages sérieux.

Ptilinus pectinicornis L. occupe en Espagne le nord du pays; il attaque électivement les troncs morts de hêtre, de peuplier et d'autres non résineux, mais ses ravages peuvent s'exercer, bien qu'exceptionnellement, dans le bois ouvré. En ce qui concerne *P. fuscus* Geoffr. les seuls exemplaires connus de l'Espagne ont été pris tout récemment à Castelltorsol (Barcelone) dans une vielle poutre attaquée, assez massivement, par cet insecte.

Eutheca solida Kiesw. est une espèce particulière à la péninsule ibérique où elle est localisée

dans la région cantabrique, la Galice et le Portugal. On la trouve à l'intérieur des habitations dans le bois ouvré, souvent très abondante au point de commettre des dégâts analogues à ceux de l'*Oligomerus ptilinoides* dans la région méditerranéenne.

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THE FRASS OF NORTHEASTERN UNITED STATES POWDER POSTING BEETLES

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Insect frass can be characterized by several criteria. The first of these is the presence of wood fragments, their size, shape and other characteristics. The second is the presence of fecal pellets, their proportion to non-fecal wood elements, their size and color. Third is the tenacity or looseness with which the frass is held within the tunnels. Finally there are some species which have such peculiar characteristics that they can be identified at once with little doubt. Such identification is deemed useful not only for systematic studies, but also for morphology, ecology and physiology; the frass and its physical and chemical characteristics can be a variable source of information relating to the natural function of each species.

Representative of the true "powder post" beetles (Lyctidae):

Lyctus planicollis Lec.: frass of very fine fragments, generally smaller than for most other species, but not so small as to distinguish easily from frass of *Ptilinus ruficornis* and *Xylobiops basilaris* which is held tightly in the tunnels, while *Lyctus* frass flows freely when wood is jarred (see Table 1 for size characteristics).

Representatives of Anobiidae are:

Hadrobregmus carinatus (Say). Frass containing both fecal pellets and discarded wood fragments, all held loosely in tunnels; pellets variable in color, from dark brown, often glistening with inclusions, to light buff wood color.

Platybregmus canadensis Fisher. Frass very similar to *H. carinatus* except for larger pellets.

Trypopitys sericeus (Say). Pellets and discarded fragments uniform brown, due to high moisture content of wood permitting growth of fungi; pellets oval in cross-section—cross-section dimension $0{\cdot}3 \times 0{\cdot}19$ mm.

Anobium punctatum Deg. (Introduced sp.). Frass includes pellets and discarded fragments of a uniform buff color.

Ptilinus ruficornis Say. Unlike other anobiids, frass packed very tightly in tunnels with no discrete pellets. Distinguished from that of *Lyctus* by its tenacity.

Xestobium rufovillosum (Deg.). Pellets bun-shaped and many stained darker on one side in a central broad band.

Representatives of the Bostrichidae are:

Xylobiops basilaris (Say). Frass similar to that of *P. ruficornis* but fragments slightly larger. Cross-sectional dimensions of largest larval tunnels (3·23 mm.) larger than that of *P. ruficornis* (2·85 mm. max.).

Stephanopachys rugosus (Oliv.). Larva lives in both bark and wood; thus frass bicolored, with dark bark elements and light wood elements. Some fecal pellets in tandem, and there are considerable amounts of brown wood fragments.

Two cerambycids, among others, cause powder posting which may superficially appear like the examples above:

Callidium antennatum Newm. Frass very similar to *S. rugosus*, but pellets and fragments considerably larger; also lacks brown fragments.

Hylotrupes bajulus (L.). Frass a mixture of fragments and pellets, uniformly wood colored; pellets truncate irregularly.

A curculionid and a scolytid are included because of the presence of the former (*Stenoscelis brevis* (Boh.)), in cases easily mistaken for anobiid damage and the peculiar characteristics of the latter (*Chramesus hickoriae* Lec.). *S. brevis*, being a small species, produces the smaller pellets; *C. hickoriae* frass contains many C-shaped, wood colored fragments as large as the fecal pellets.

Two families associated with very moist wood, often with advanced stages of wood decay are the Cupedidae and the Oedemeridae. These both produce frass of uniform, dark brown color, darker than the wood.

TABLE 1.
Frass of Common Powder Post Beetles

Insect	*Dimensions of Largest Frass Particles (mm)*		
	(*a*) *Length*	(*b*) *width*	*Ratio* (*a*):(*b*)
ANOBIIDAE			
Hadrobregmus carinatus (Say)	·82	·45	1·82
Platybregmus canadensis Fisher	1·05	·45	2·33
Ptilinus ruficornis (Say)	·08	·08	1·00
Trypopitys sericeus (Say)	·68	·30 (Broad)	2·27
		·19 (Narrow)	3·57
Anobium punctatum (DeG.)	·38	·15	2·53
Xestobium rufovillosum (DeG.)	1·05	1·05 (Broad)	1·00
		·53 (Narrow)	1·98
BOSTRICHIDAE			
Xylobiops basilaris (Say)	·10	·10	1·00
Stephanopachys rugosus (Oliv.)	·75	·38	1·97
LYCTIDAE			
Lyctus planicollis Lec.	·08	·08	1·00
CURCULIONIDAE			
Stenoscelis brevis (Boh.)	·15	·08	1·88
SCOLYTIDAE			
Chramesus hicoriae Lec.	·90	·45	2·00
CERAMBYCIDAE			
Hylotrupes bajulus (L.)	1·28	·75	1·71
Callidium antennatum Newm.	·82	·38	2·16
CUPEDIDAE			
Cupes sp.	·75	·61	1·23
OEDEMERIDAE			
Nacerda melanura (L.)	·75	·31	2·42

FUMIGATING WITH VIKANE

H. E. GRAY

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Sulfuryl fluoride as a compound is old in the chemical literature, however, its insecticidal fumigant properties were not recognised until the late 1950's. Vikane fumigant (sulfuryl fluoride) is now marketed to the professional fumigators especially for use in the control of arthropod pests infesting buildings and non-edible commodities.

Sulfuryl fluoride is a highly stable, odourless, colourless non-flammable compound which boils at minus 67°F. At room temperature (70°F) the gas exerts a pressure of 237 psi. It possesses exceptional penetrability and likewise aerates quickly from treated buildings following completion of the exposure period.

Since sulfuryl fluoride is a gas at ambient temperatures, acute ingestion is highly improbable. Sufficient data have been obtained to indicate an acute oral LD50 of 100 mg/kg of body weight for male and female rats and for female guinea pigs. The greatest hazard from the liquid directly contacting the skin would be the freezing of tissues.

As a result of chronic vapour toxicity studies it has been concluded that concentration of the gas in work areas where repeated exposure is possible should not exceed 10 ppm. The time weighted average for seven to eight hour daily exposures should not exceed 5 ppm.

Sulfuryl fluoride is toxic to all stages of insect life, however with some species the egg stage is somewhat more difficult to kill.

Thermal conductivity (TC) instruments are most useful for monitoring concentrations of sulfuryl fluoride gas during the exposure period. Specially designed, inexpensive, easy-to-use equipment is available for determining when a building fumigated with sulfuryl fluoride has been aerated sufficiently to permit reoccupancy.

If it becomes necessary to enter an area where toxic concentration of sulfuryl fluoride gas may exist, respiratory protective equipment must be worn. Certain acid gas canisters will give protection for a limited amount of time. Black organic vapour canisters and some acid gas canisters will not afford sufficient protection.

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ZUR IMAGINALPARASITIERUNG FORSTLICHER CURCULIONIDAE

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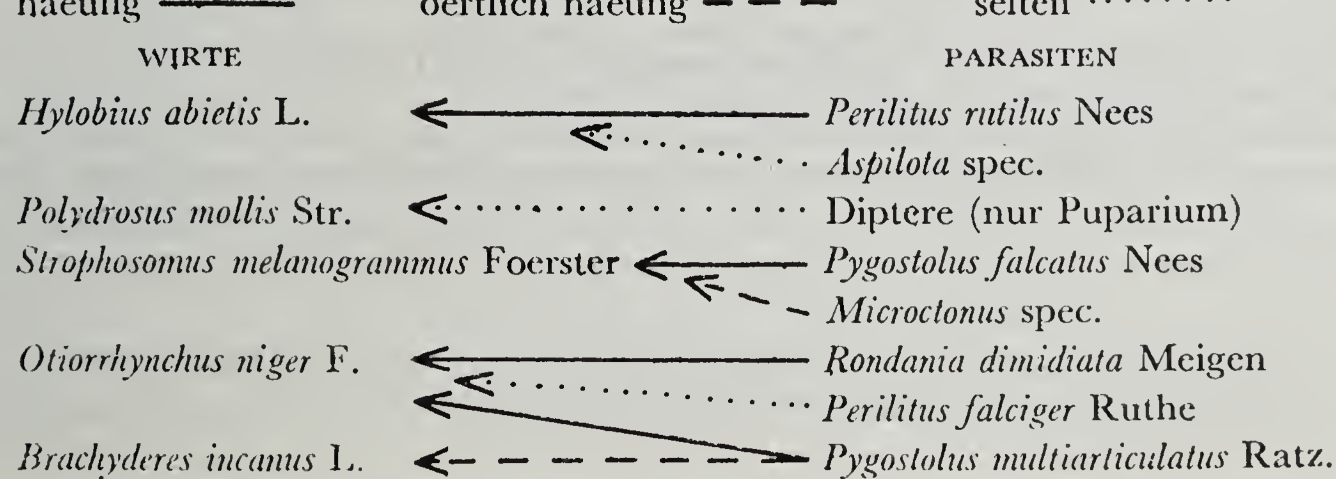
Seitdem sich bei Arbeiten ueber den rotbeinigen schwarzen Ruesselkaefer (*Otiorrhynchus niger* F.) eine nicht unerhebliche Parasitierung der Imagines gezeigt hatte (3), wurden die Untersuchungen ueber die *Imaginalparasitierung* forstlich wichtiger Ruesselkaefer (Curculionidae) forstgesetzt. Dabei ergab sich, dass die in der anschliessendenUebersicht aufgefuehrten Kaefer von folgenden Braconiden und Dipteren befallen werden:

Parasitierung:

haeufig ——— oertlich haeufig — — — selten ·······



Die Braconiden der Gattungen *Perilitus* und *Pygostolus* sowie die Tachine *Rondania dimidiata* sind als Parasiten anderer Ruessler bereits bekannt (1, 2, 4, 6, 7, 8).

Feststellungen ueber die Imaginalparasitierung, insbesondere ueber ihr zahlenmaessiges Ausmass, sind nur dann moeglich, enn eine grosse Zahl von Kaefern zu dem Zeitpunkt unter Beobachtung steht, an dem die Parasitenlarven die Wirtsimagines verlassen und sich verpuppen. Dies ist entsprechend dem Entwicklungszyklus der Parasiten ueberwiegend im Fruehjahr, bei einigen mit 2. Generation aber auch im Sommer und Herbst der Fall. Als haeufiger parasitiert erwiesen sich *Hylobius abietis*, *Strophosomus melanogrammus* und *Otiorrhynchus niger*, von denen in ueber zehnjaehriger Beobachtungszeit mehrere tausend Kaefer zu verschiedenen Jahreszeiten gezwingert und eine Reihe von Wochen in Hinblick auf Parasitierung unter Quarantaene gehalten wurden.

Die Parasiten *Pygostolus multiarticulatus*, *Perilitus falciger* und *Microctonus* spec. durchlaufen einen univoltinen, *Perilitus rutilus* und *Rondania dimidiata* einen bivoltinen Zyklus. *Pygostolus multiarticulatus* und *P. falcatus* verlassen ihre Wirte Anfang Mai bis Anfang Juni. Die Kokonruhe der zuerst austretenden Tiere dauert 2-3 Wochen, die der spaeter kommenden dagegen entsprechend der ansteigenden Temperatur nur 8-12 Tage. Die Larven der 1. Generation der bivoltinen *Perilitus rutilus* und der *Rondania dimidiata* verlassen ihre Wirte schon ueberwiegend im April, haben eine etwa dreiwoechige Kokonruhe und schluepfen in der Masse Mitte Mai. Die 2. Generation der Diptere fliegt in der Mitte des Sommers, diejenige von *Perilitus rutilus* kann noch im Herbst des ersten Jahres schluepfen (und trifft dann auf die um diese Zeit oft in grosser Zahl auftretenden Jungkaefer des *Hylobius abietis*).

Coparasitierung (5) wurde nicht beobachtet, wird aber fuer moeglich gehalten. Eine *Superparasitierung* durch mehrere Individuen einer Parasitenart war dagegen fast immer die Regel. Sie fuehrt jedoch lediglich bei den kleineren Parasitenspecies zur erfolgreichen Entwicklung mehrerer Parasiten in einem Wirt.

Im grossen Durchschnitt erwiesen sich bei Einzeluntersuchungen kaum mehr als 10% der Ruessler als befallen. In bestimmten Faellen ist der Parasitenbesatz aber wesentlich hoeher. So waren 940 Exemplare von *Strophosomus melanogrammus* im Mai 1959 zu 27% durch *Microctonus* spec. parasitiert. Auch bei *Otiorrhynchus niger* lag der Befall haeufig ueber 10%, insbesondere durch *Rondania dimidiata*. Man muss hierbei beruecksichtigen, dass bedingt durch die schwierigen Beobachtungsmoeglichkeiten immer nur eine mehr oder weniger "momentane Parasitierung" aufgedeckt wird. Schaetzungsweise kann die Parasitierung im Ganzen bis zu 50% betragen (bei ermitteltem 10% igem Besatz) und in den Beobactungsreihen mit festgestellter 20% iger Parasitierung duerfte sie bis zu 90% im Ganzen ansteigen. Diese relativ hohen Zahlen ergeven sich aus der Tatsache, dass die Ruesselkaefer ueberwiegend eine zweijaehrige Lebensdauer haben und bei den Untersuchungen im Fruehjahr mehr als die Haelfte des Materials aus noch nicht parasitierten Jungkaefern besteht, so dass die Parasitierung bei "Momentaufnahmen" selten 25% ueberschreiten kann.

Die mitgeteilten Ergebnisse lassen erkennen, dass die Imaginalparasitierung bei den Ruesselkaefern einen wichtigen Faktor von forstwirtschaftlicher Bedeutung fuer die Erhaltung des biologischen Gleichgewichts darstellen kann.

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BEITRAG ZUR KENNTNISS DER FRUCHTBARKEIT DES BRAUNEN RÜSSELKÄFERS (*HYLOBIUS ABIETIS* L.)

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Eine der wichtigen Fragen bei der Massenvermehrung des Rüsselkäfers ist die Fruchtbarkeit, die zusammen mit der Gonadenentwicklung beider Geschlechter an den im Labor gezüchteten Populationen (Temperatur 20-28°C, relative Feuchtigkeit 90-96%) untersucht wurde.

[Zuchtergebnisse: Eistadium durchschnittlich 15 Tage, Larvenstadium 58-82 Tage, durchschnittlich 73 Tage, Puppenstadium ungefähr 19 Tage, Gesamtentwicklung zur Käferschlüpfung 3-4 Monate, im Durchschnitt 107 Tage. Diese Periode deckte sich mit den einzeln vorkommenden Fällen der einjährigen Generation (warmes Elbetals Sandgebiet); die Generation ist in der Tschechoslowakei meistens zweijährig (14-15 1/2 Monate, durchschnittlich 413 Tage)].

Die Sezierungen der frisch geschlüpften Weibchen zeigten, dass diese, obwohl mit leerem Verdauungstrakt, reichlich entwickelte Fettkörper aufwiesen. Ihre Eiröhre sind bisher nicht differenziert und enthalten nur die Oogonien. Der Fettkörper der frisch geschlüpften Männchen ist auch reichlich entwickelt, aber die Entwicklung der Gonaden ist fortgeschrittener: die Folikulen des Testes enthalten schon die Spermatozysten mit den Spermatozyten.

Ungefähr nach einem 15-18 Tage langem Aufenthalt der Käfer in den Puppenkammern war der Fettkörper beider Geschlechter fast konsumiert. Während bei den Männchen schon ausser den Spermatozyten auch die Bändchen der Spermien und vereinzelte loose aktive Spermien vorgefunden wurden, änderte sich der Stand der Eiröhre von Weibchen nicht.

Um die Abhängigkeit der Geschlechtsreife besonders der Weibchen an der Frassintensität und der Frasszeit festzusetzen, wurden die Rüsselkäfer einerseits unter direkten Zugang zur Nahrung, andererseits unter minimalen Gaben, die nur die Lebenserhaltung von Käfern sichern, gezüchtet. Dabei wurde sowohl sexuelle Isolation als auch das Zusammenleben beider Geschlechter eingehalten. Die Existenz dieser Abhängigkeit wurde nur bei der Weibchen bestätigt.

Die Testes enthielten auch bei den hungernden Männchen schon von den ersten 14 Tagen aktive Spermien. Die Differenziation der Eiröhre der hungernden Weibchen begann jedoch erst nach drei bis vier Wochen—nur vereinzelt entstehende Oozyten der I. Klasse wiesen jedoch bei den hungernden Weibchen den Wuchs nicht einmal nach der Bildung des schwachen Fettkörpers nach drei Monaten auf.

Bei den gefütterten Käfern wurde das intensivere Konsumieren der Nahrung, besonders in den Anfangsphasen bei Weibchen, die schon nach einwöchigem starkem Frass verhältnissmässig reichen Fettkörper, die Differenziation der Ovariolen und die Bildung der Oozyten zeigten, verzeichnet. Im Laufe der zweiten Woche erschienen die ersten legefertigen Eier. Die Gelbkörper wurden bei etlichen Weibchen schon nach 23 Tagen des Frasses verzeichnet.

Aus dem erwähnten ist die Notwendigkeit der intensiven Reifefrasse, besonders bei den jungen Weibchen, klar: diese Erfahrung zeigte, warum in einigen Jahren mit dem für die Entwicklung günstigen Wetter Ende Sommer oder Anfang Herbst rasch zu starker Beschädigung der Kieferkulturen erst am Ende der Vegetationsperiode kam.

Die Fruchtbarkeit der Weibchen wurde in Laborversuchen (Feuchtigkeit 96%, Temperatur 16-28°C) untersucht.

[Ergebnisse: Eiablageperiode 110 Tage; durchschnittliche Menge der pro Tag und 1 Weibchen geleten Eier: Mai—0,8, Juni 2,1-2,3, Juli 1,4, August 0,8; Gesamtzahl der Eier: min. 33, max. 183 Stück. Die Bewegung der Eiablage in den Gränzen von 86 bis 150 Stück, im Durchschnitt 118 Eier pro 1 ♀ (statistische Bewertung bei 95% Sicherheit)].

Die anatomische Untersuchung (115 Käfer) stellte in 15 bis 16% Fällen Endoparasiten, die klaren Einfluss auf die Herabsetzung der Fruchtbarkeit ausübten, fest (bis 22 Larven pro 1 Käfer).

Aus dem Angeführten geht hervor, dass bei genügender Menge geeigneter Nahrung und den günstigen klimatischen Bedingungen die Reproduktionfähigkeit des Rüsselkäfers erheblich ist.

SECTION 11.—INSECT PATHOLOGY AND RELATIONSHIPS BETWEEN INSECTS AND MICRO-ORGANISMS

The following paper was read but the author did not wish it to be published here: Hoogstraal, H. (U.S.A.). *Leishmania* and flagellates in *Phlebotomus* in Upper Nile, Sudan.

EXPERIMENTAL TECHNIQUES IN INSECT PATHOLOGY

NEW TECHNIQUES FOR THE STUDY OF INSECT-TRANSMITTED PLANT VIRUSES

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1. *Rearing of aseptic leafhoppers.*

The following 4 species of leafhoppers were used: *Macrosteles fascifrons*, *Dalbulus maidis*, *Agallia constricta*, and *Agalliopsis novella*. Mated females were confined in small leaf cages magnetically attached to limited areas of host plants for oviposition. Deposited eggs were excised from leaf tissues, fastened to strips of wax paper, surface sterilized, and placed in culture tubes containing plants grown on agar from sterilized seed. The developmental cycle of all four species was completed in approximately the same period as under natural conditions at the identical temperature. Consecutive generations were reared in the same manner as the first generation, and insects were transferred from vessel to vessel aseptically (1).

2. *Inoculation of aseptic insects with aster yellows virus.*

In order to obtain aseptic viruliferous insects, aster yellows virus was first transmitted to plants grown aseptically. This was accomplished by moving a leaf from an aseptically grown plant upward in the culture tube and drawing it partly out from the tube. Virus carrying leafhoppers were confined for 4 days to the protruding leaves. Aster yellows symptoms appeared in plants inside the tubes after 2 to 4 weeks. Afterward, virus-free insects from aseptically reared stock were confined to aseptic diseased plants. Once the insects acquired the virus, they transmitted it easily to fresh aseptic seedlings (2).

3. *Feeding of insect vectors on artificial media by the wick-feeding technique.*

A special container was devised for aseptic rearing of leafhoppers on synthetic diets. A diet consisting of amino acids, vitamins, salts, and sucrose was supplied by means of a gauze wick. The following vitamins were also incorporated: choline, folic acid, inositol, nicotinamide pantothenate, pyridoxal, riboflavin, and thiamine. Furthermore, the medium contained potassium phosphate, magnesium chloride, and cholesterol. When third instar leafhopper nymphs were given access to this synthetic diet, they molted but their further development was retarded and death usually occurred after 15 days. Adults survived well on the wick-supplied medium (3).

4. *Maintenance of insect vectors on plant tissues* in vitro.

Tomato, potato, and carrot tissue cultures were used to feed aseptically reared *M. fascifrons*. The leafhoppers survived particularly well on carrot root tissue. Adults were maintained for 6 weeks and they deposited eggs from which first instar nymphs hatched, but these in turn did not survive, probably because of excessive moisture. Second instar nymphs, placed on carrot tissue, molted into third, fourth, and fifth instar nymphs and finally became adults, then mated and deposited eggs (4).

5. *Inoculation of plant tissues* in vitro.

A simple technique was devised to permit the *in vitro* inoculation of plant tissues with viruses that ordinarily require insect vectors for transmission *in vivo*. Viruliferous aseptic *M. fascifrons*, obtained in the manner described above (2) were confined to cultured carrot root tissues for 20 days. Although the exposed tissue grew well and did not seem to differ from uninoculated controls, virus-free aseptic *M. fascifrons* recovered virus from this tissue, proving the successful transmission of aster yellows virus to cultured carrot root tissues (5, 6).

6. *Recovery of virus from excised organs of vectors.*

To study the site of virus multiplication and storage in insect vectors, inoculated *M. fascifrons* were dissected and the following organs removed and placed in culture medium: salivary glands, Malpighian tubules, guts, and gonads. Virus recovery was attempted from freshly excised organs as well as from organs maintained *in vitro* for 14 days. The bioassay technique used was as follows: the various organs were washed in sterile salt solution, crushed, and homogenized, and the extract centrifuged in sealed capillary tubes. The supernatant fluids were injected into virus-free leafhoppers, and the inoculated insects were tested weekly on fresh lots of susceptible plants. Because of technical difficulties in the separation of fat body tissues, this organ was not included. Malpighian tubules yielded virus after having been maintained *in vitro* for 14 days; gut contained virus shortly after insects acquired it, but not later; salivary glands yielded only small amounts of virus 5 days after insect inoculation, but provided an excellent source of inoculum after 19 days (7).

7. *Cultivation of embryonic leafhopper cells.*

Attempts were made to cultivate embryonic leafhopper cells, obtained from dissected eggs of *M. fascifrons* at various stages of development. A minimum of 100 eggs in the same developmental stage was used for each test. The surface-sterilized eggs were cut open under a dissecting microscope and the embryos gently removed into the culture medium. After several washings, the embryos were trypsinized with a 0·02 per cent trypsin solution and resuspended in culture medium. Sitting drop cultures were set up in small V-H type culture vessels. The blastokinetic movement stage, obtained approximately eight days ofter oviposition, yielded growing cells of seven different types (8, 9).

8. *Rapid insect injection technique.*

The use of insect injections has provided a method for assaying virus preparations in numerous leafhopper borne and certain aphid borne viruses. The original inoculation technique, which was cumbersome and time consuming, was modified so as to facilitate the injection of large numbers of insects in a short time. The mechanical inoculation was carried out on a specially constructed stage equipped with a series of 20 spring-type holders fastened to an adjustable bar. The springs of the holders were adjustable, permitting gentle immobilization of insects. A single operator, using four mechanical stages, can inject up to 4,000 insects in one day (10).

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LES RICKETTSIOSES D'INSECTES

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Introduction. L'étude des rickettsioses a été abordée au point de vue entomologique d'abord à cause du rôle de vecteur joué par certains insectes, ensuite parce que certaines d'entre elles ont été reconnues comme pathogènes aux insectes. Actuellement, on connaît cinq espèces, affectant des insectes appartenant à trois ordres. Chez les Coléoptères, ont été décrites des rickettsioses sur *Popillia japonica* Newm. (1, 2); *Melolontha hippocastani* Fabr. et *M. melolontha* L. (14, 4, 11), chez les Diptères *Tipula paludosa* Meig. (9); enfin chez les Orthoptères une rickettsiose de *Gryllus* a été récemment montrée (13).

Le développement des recherches dans ce domaine, dépend en grande partie de l'évolution des méthodes étroitement adaptées à la spécialité.

Recherche des corps rickettsiens et pathogénèse. Les symptômes externes (irisation, hypertrophie) peu caractéristiques, ne permettent pas de conclure sur l'origine de la maladie.

L'observation de frottis légers réalisés par empreintes des organes et colorés suivant les techniques de Macchiavello ou de Giemsa est nécessaire. L'examen plus approfondi est donné par l'histologie normale et électronique.

En vue d'étude histologique les individus malades sont fixés dans le Carnoy, permettant la coloration de Feulgen; les amas de rickettsies apparaissent alors en rouge. Nous avons obtenu d'excellents résultats, après fixation au Bouin, et coloration par la méthode de Ramon y Cajal et par celle de la fuschine anilinée—bleu de méthylène (12). Ces techniques permettent la localisation des agents et l'étude de leur pathogénèse.

En microscopie électronique, la méthode de frottis (soit colorés négativement à l'acide phosphotungstique, soit examinés directement ou après ombrage au palladium) permet l'étude de la forme des rickettsies et de leur taille. L'histologie électronique met en évidence les zones de multiplication et leur structure. Des fragments de tissu adipeux sont fixés à l'acide osmique à 1% dans le tampon véronal à pH 7,4 à 4°C, pendant 4 heures, deshydratés dans la série des alcools et inclus dans des métacrylates, l'araldite ou l'épon.

Ces méthodes font apparaître des analogies et certaines différences entre les affections rickettsiennes des insectes.

Les ressemblances sont la taille (600 mμ de long sur 300 mμ de large) la disposition souvent en chaînettes à l'intérieur des vacuoles cytoplasmiques et l'atteinte progressive des différents tissus.

Parmi les différences, nous citerons le polymorphisme moins accentué pour *R. grylli* et surtout la présence ou l'absence d'un cristal rhomboïde qui accompagne la multiplication des rickettsies de Coléoptères et de Tipule, mais qui est absent dans le cas de la rickettsiose des gryllidées. Ce cristal bipyramidal manifeste une double structure qui apparaît en histologie après coloration de Giemsa ou sur coupes colorées à la phloxine-bleu de méthylène et en microscopie électronique mettant en évidence un pôle fortement coloré et une zone moins dense.

Il semble que ce cristal proviendrait des granulations albuminoïdes dont il a la même composition en acides aminés à l'exclusion de la tyrosine (5), il serait un élément néoformé du à une déviation du métabolisme de l'hôte créée par la présence des rickettsies. D'autre part, lors des infections en culture de tissus de vertébrés par la rickettsie de *Melolontha* (10) on a constaté la multiplication des rickettsies, mais non la formation du cristal.

Diagnostic. Il nécessite la reconnaissance des symptômes externes et internes et l'observation des agents pathogènes au microscope optique, après les colorations diverses. Cependant, la petitesse des rickettsies, impose l'usage du microscope électronique.

Examen de virulence. Un autre aspect des rickettsies est leur spécificité et leur spectre de virulence. La rickettsie de *Melolontha* infecte plusieurs espèces de Scarabéides mais reste sans action vis-à-vis des larves de diverses cétoines (3). *Rickettsiella grylli* a un spectre d'action large sur les Orthoptères lors d'infection "per os".

De notre côté, nous avons constaté une action positive de *R. grylli* sur les Orthoptères, mais également sur le Coléoptère *M. melolontha* aussi bien par ingestion forcée au moyen d'une

seringue à aiguille rodée que par inoculation. La lyse du tissu adipeux, une perte de turgescence et une pseudotransparence des larves sont observées (7).

R. grylli peut même se multiplier sur le Lépidoptère *Galleria mellonella* L. après inoculation. Le tissu adipeux est transformé, mais l'infection de larves âgées, n'empêche pas la métamorphose et la ponte (8). Son spectre de virulence est donc vaste chez les insectes.

Des essais ont été tentés sur Vertébrés. L'infection nasale à des souris entraîne la multiplication des rickettsies dans le poumon. Cependant, on assiste à une perte progressive de virulence, après quatre passages (10).

Par voie intrapéritonéale à des souris gravides les rickettsies déclenchent l'avortement (6). Ce fait serait à rapprocher de l'action des rickettsies des ovins qui amènent elles aussi l'avortement des brebis.

Infection de cultures de tissus. La culture des rickettsies de mammifères sur cellules homologues est difficile. Des essais d'infection de cellules animales avec *R. melolonthae* ont cependant été tentés avec succès (10). Nous étudions actuellement, l'infection "in vitro" de cellules de Lépidoptères par rickettsies déjà adaptées à *Galleria* par passages successifs, afin de poursuivre l'étude de la pathogénèse cellulaire.

Purification et conservation des rickettsies. Des fragments de tissus adipeux de larves atteintes sont mis en suspension dans l'eau physiologique et fortement pipetés. La séparation des rickettsies s'effectue par centrifugations différencielles dont la dernière à 6,000g permet leur sédimentation.

Les souches rickettsiennes, peuvent être conservées en plaçant au congélateur à –30°C, les individus atteints. Cette méthode simple n'entraîne pas de baisse du taux de virulence après plus d'un an de conservation.

Conclusions. Les différentes techniques que nous venons de décrire, laissent envisager plusieurs sujets de recherches:

—l'emploi de plus en plus généralisé du microscope électronique pour l'établissement du diagnostic permettra des prospections plus poussées dans la recherche de ces affections, chez de nouvelles espèces.

—les progrès récents en culture de tissus d'invertébrés laissent espérer la possibilité de l'étude de la pathogénèse rickettsienne "in vitro".

—enfin avant d'envisager l'utilisation de ces agents pathogènes aux insectes, pour une éventuelle lutte biologique, il est souhaitable de dégager plus nettement les notions de spécificité et de virulence, chez des hôtes non habituels et surtout les vertébrés.

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ELECTROPHORETIC ANALYSIS OF ESTERASES AS AN AID TO THE CLASSIFICATION OF *BACILLUS THURINGIENSIS*

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The characterisation of multiple molecular enzyme systems by electrophoresis in starch gel and polyacrylamide gel is providing the biologist with new criteria for taxonomic studies. So far these methods have found little application in microbial taxonomy but starch gel electrophoresis of esterases is now being studied in several bacterial groups.

The protein crystal-forming bacteria have distinctive multiple esterase systems and may be divided into groups on a basis of the presence or absence of particular esterase bands when disintegrates of vegetative cells are analysed by electrophoresis in starch gel using a discontinuous tris-citrate/borate buffer system.

Some 70 different isolates have been studied using biochemical tests, H (flagellar) antigen composition and esterase analysis. The results show a high correlation between the antigenic and esterase methods and are summarised in table 1.

Table 1

Comparison of biochemical, serological and esterase characteristics of crystal-forming bacteria

Serotype	*H. antigens*	*Biochemical reactions*					*Esterase pattern*
		Acetylmethylcarbinol production	*Lecithinase*	*Acid from salicin*	*Acid from sucrose*	*Hydrolysis of starch*	
1	I	+	+	+	+	+	Berliner
2	II	+	+	+	+	−	Finitimus
3	III	+	+	−	−	+	Alesti
4A	IV, a	+	+	−	+	+	Sotto
4A	IV, a	+	+	−	−	+	Dendrolimus
4B	IV, b	+	+	+	−	+	Kenya
5	V	+	W	+	−	+	Galleriae
6	VI	−	−	−	+	+	Entomocidus
6	VI	+	−	−	+	+	Entomocidus
7	VII	+	+	+	−	+	Galleriae
8	VIII	+	−	−	+	+	Morrison
9	IX	+	+	+	−	+	Tolworth

W = reaction weak and variable.

Esterase analysis separates the *sotto* and *dendrolimus* bacteria in Serotype 4A but fails to separate Serotypes 5 and 7. It agrees with the antigenic analysis in placing biochemically different isolates in Serotype 6. In all other cases there is complete agreement between the antigen and esterase classifications.

Unlike the majority of biochemical tests both antigen and esterase methods are concerned with the structure of protein molecules rather than simply with their function, and the results may be related more directly to the genetic processes controlling the synthesis of proteins in the cell. For this reason it is suggested that sub-groups defined by these methods are biologically significant ones and should be accorded more weight than divisions based only on classical biochemical reactions.

SOME ASPECTS OF THE MECHANISMS OF PATHOGENICITY OF BACTERIA PATHOGENIC FOR INSECTS

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Bacterial and other pathogens should be classified according to their relationships with their hosts. A fundamental knowledge of these relationships is needed so that future work will be less empirical than it has been. Some schemes for classification on this basis have been developed, e.g. by Steinhaus, Bucher and Weiser and Lysenko. They are correct to some extent as crude generalisations, although pathogenicity itself remains difficult to explain by such schemes. The present schemes of classification of insect pathogens are based on analogies with other fields of pathology. This, however, may not be valid because insect diseases have been categorised empirically rather than by fundamental knowledge of the host-parasite interactions, which are still largely unknown. A knowledge of the chemical nature of the toxins of *Bacillus thuringiensis* Berliner, for example, would help to explain its selective pathogenicity. Except for lecithinase, however, we do not know what these toxins are. Information about them would help, not only to classify the mechanisms of pathogenicity of *B. thuringiensis* but to make comparisons with other pathogens.

Some progress has been made in the identification of the mechanism of pathogenicity of *Pseudomonas aeruginosa* (Schroeter) Migula in larvae of *Galleria mellonella* Linnaeus. Previous work (Lysenko, 1963) showed the bacterium produced a toxic antigen which killed larvae when injected into their body cavity. The toxin from culture filtrates was studied by means of starch electrophoresis, absorption chromatography, gel filtration and precipitation with ammonium sulphate. All these methods gave very similar results. Best separation was achieved by gradient elution of the filtrate on DEAE-cellulose and subsequent gel filtration of the active fraction with Sephadex G-75. The toxic fraction was proteolytic, as measured by the azo-casein method. This was supported by a correlation between proteinase activity and LD_{50} of culture filtrates during cultivation of the bacterium.

Proteolytic activity is a common characteristic of many bacteria and Bucher has assumed that bacteria that showed most proteolytic activity against gelatine were the most pathogenic. I have found, however, that strains of *Pseudomonas aeruginosa* which exhibited the same ability to digest gelatine, were very different in their LD_{50} or LD_{99} in the same host. Similarly, crystalline proteinase from *Bacillus subtilis* had the same activity as that from *P. aeruginosa* on azo-casein but it was only about one tenth as toxic. These results support those of Morihara who showed that proteinases from different bacterial species were serologically different. It is clear that results of workers in fields other than insect pathology, such as these of Morihara, are relevant to the problems of bacterial toxins and the conditions under which they are produced. Much progress will occur in insect pathology when the toxins of insect pathogens are identified by the many modern routine methods of biochemistry and microbiology that are now available.

INSECT TISSUE CULTURES FOR THE STUDY OF SILKWORM NUCLEAR POLYHEDROSIS VIRUS

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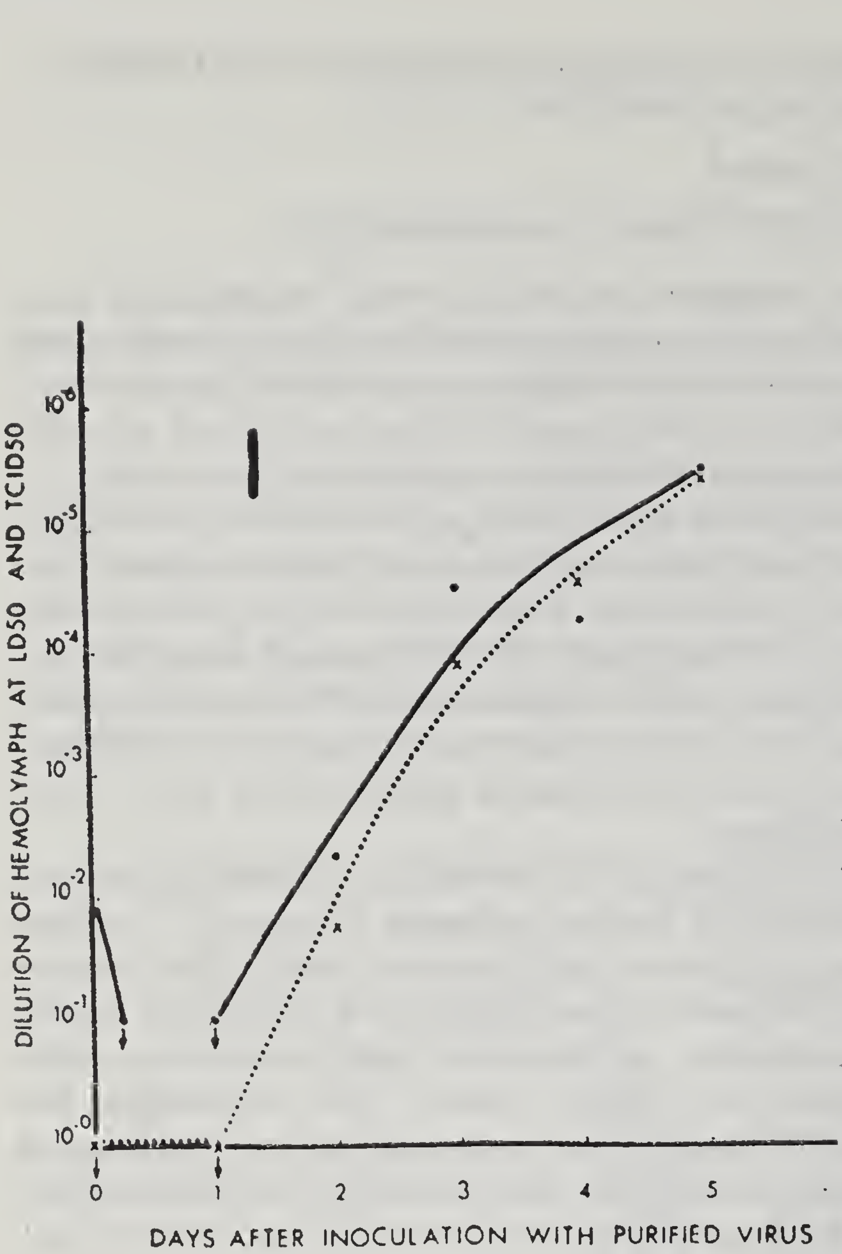
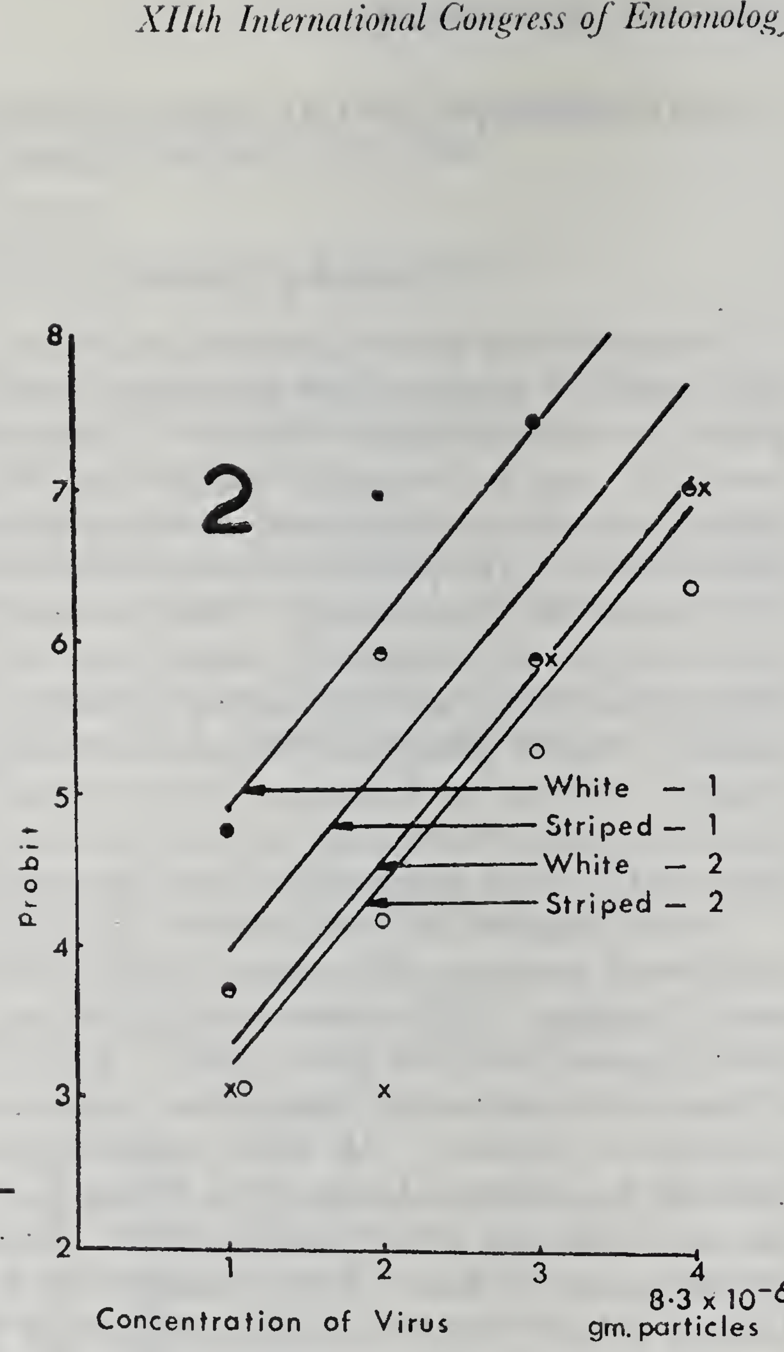
Many types of study with insect viruses require a standardised method for assay of viral infectivity. Conventional methods require large numbers of insects at a particular stage of development in order to obtain reliable measurements of LD_{50}. In the method we have used it is possible to obtain eight cultures from one insect—thus the whole assay can be set up using a small group of insects. In a classical paper on the nuclear polyhedrosis of the silkworm Bergold demonstrated that when inclusion bodies taken from diseased larvae are dissolved in





Insect Strain and Virus Preparation	Striped 1	Striped 3	White 1	White 3
Calculated ID_{50}.	1·82	2·08	1·17	2·57

COMPARISON OF SELECTED PAIRS OF ID_{50} VALUES

Tests compared	$\bar{x}$ = mean difference	Standard error = σ	No. of S.E = $\frac{\bar{x}}{\sigma}$	P.
W1 with W3	1·42	0·322	4·4	·00635%
W1 with S1	0·77	0·293	2·6	0·932%
W1 with S3	0·91	0·327	2·8	0·511%
W3 with S1	0·77	0·910	0·9	36·81%
S3 with S1	0·26	0·937	0·3	>50·0%

S.E = Standard Errors

P. = Probability of occurrence of a deviation as great as or greater than designated number of standard errors.

3

FIGS. 1, 2 and 3. Silkworm nuclear polyhedrosis virus. (1) Time course of virus multiplication in infected silkworm; (2) Susceptibility of insect tissue cultures derived from "white" or "striped" silkworms to two insect virus preparations; (3) Comparison of selected pairs of $TCID_{50}$.

dilute sodium carbonate solutions at about pH 10·5, virus particles are released, and that these particles and not the polyhedron protein solution are responsible for initiating infection.

Inclusion body virus disease may be transmitted in the laboratory by the following methods:

A. A suspension of polyhedra may *be fed* to a healthy larva. Insects are readily infected when polyhedra are taken in with the food. Washed polyhedra fail to initiate infection when injected into a caterpillar, presumably because the pH of the haemolymph is not high enough to release virus particles.

B. Suspensions of virus particles prepared by dissolving polyhedra may be *injected* into the haemocele. The insect usually succumbs with symptoms of the disease in 5-10 days.

C. Blood from infected larvae may be inoculated into insects. This mode of infection has been used frequently by microbiologists to passage a particular insect virus.

In this paper we report on the susceptibility of insect tissue cultures to haemolymph from infected insects and to suspensions of virus particles obtained from inclusion bodies.

Techniques.—Primary explants of ovaries from fifth instar silkworm larvae were cultured in Leighton tubes (Vaughn and Faulkner, 1963, Virology, 20, 484-9).

Most of the silkworm tissue culture media have been based on analyses of silkworm haemolymph. We used the medium described by Jones and Cunningham (Nature, 1960, 187: 1072-4) in which amino acids are present in a lactalbumen hydrolysate.

In the initial stages of this work we were interested in comparing the infectivity of a particular virus preparation when assayed in living insects by measuring the LD_{50}, and in tissue cultures by measurement of Tissue Culture Infectious Dose 50% ($TCID_{50}$).

Figure 1 is a diagram which shows the time course of virus multiplication in the living insect. Groups of twelve caterpillars were injected at zero time with 100 LD_{50} of purified virus and at various intervals blood was collected from a group of larvae and assayed both *in vivo* and in tissue cultures. The results are in agreement with other workers and show that using either method it was possible to detect an eclipse phase when no infectious material is released into the haemolymph, and also that both methods detect the logarithmetic increase of virus into the haemolymph as the insect becomes heavily infected. We conclude that insect tissue cultures are susceptible to virus present in haemolymph and yield infectivity data comparable with that obtained *in vivo*.

The virus particles derived by the dissolution of inclusion bodies in dilute sodium carbonate were also used as inoculum for our studies. The *in vivo* LD_{50} of such a suspension of virus in fourth or fifth instar larvae is approximately 5×10^{-12} gms. virus per larva. If a standardised injection technique is used there is little variation between experiments. When we first infected insect tissue cultures with these highly infective virus suspensions we obtained erratic results. In some experiments 10^6 LD_{50} of particles failed to infect our cultures, whereas in other experiments dilutions of virus particles containing 10^4 LD_{50} per culture gave a 50% tissue culture infectivity end point, which was the same order of infectivity obtained when haemolymph was the source of virus. Also in some of our earlier experiments we found that the presence of inclusion body protein with the virus particle suspension enhanced the infectivity of particles.

The inconsistencies observed when tissue cultures were infected with particles may be due either to small differences in composition of the tissue culture medium, or to slight difference in the degree of infectivity of a particular virus particle preparation. It was also possible that ovaries from different families of silkworm had a varying degree of susceptibility to the virus. We endeavoured to test this latter point since we had available two inbred strains of silkworm designated "white" and "striped". A number of experiments were set up to determine whether tissue cultured from these strains were equally susceptible to a particular virus preparation.

Two virus particle preparations were assayed using tissue cultures obtained from either "white" or "striped" silkworms. The medium was that of Jones and Cunningham supplemented with heated haemolymph from the appropriate insect strain. Usually ten replicate cultures of each of four virus concentrations were used in titration. The results were scored as positive if polyhedron bodies were found in the explant after incubation at 26° for seven days.

The percentage of infected cultures at each dilution was converted to probits and plotted

against the concentration of virus. A common slope was then calculated. It was found that none of the data differed significantly from a probit line with this slope. Probit regression lines having the common slope were then plotted for each set of data. These lines are shown in Fig. 2.

Certain selected pairs of ID_{50} values were analysed to determine if they were statistically different. The results given in Fig. 3 show that the ID_{50} for "White 1" is statistically different from the ID_{50} of "White 2", "Striped 1", and "Striped 2". No other significant differences were found, possibly because the data are somewhat limited.

The results indicate that tissue cultures derived from different families have the same general response to virus particles, as shown by the common slope of the probit regression lines. There is a variation in the degree of susceptibility between families of silkworm regardless of the strain, as shown, for example, by the fact that tissue from insects from family "White No. 1" was significantly more susceptible to virus particle suspensions than all other families. That this variation is not strain dependent is demonstrated by the fact that in the first virus preparation the "White" strain was different in susceptibility from the "Striped", but in the second experiment no difference was detected.

We conclude that individual virus preparations prepared using the same conventional technique have unpredictable differences in infectivity. The difference in infectivity of particles may be due to slight variations in the method of preparation, to minor differences in the insect tissue culture medium or the differences in susceptibility of tissues from different families.

INFLUENCE OF ENVIRONMENTAL FACTORS ON INSECT DISEASE

ENVIRONMENT, NATURAL SELECTION, AND BALANCE IN PATHOGEN-HOST SYSTEMS

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Genetic evolution occurring in pathogen-host systems results in integration and balance between these species in nature. The genetic feed-back mechanism leads to the regulation of insect pathogen numbers and the gradual evolution toward ecological homeostasis with its insect host (Amer. Naturalist, 1961). It operates through a density-dependent interaction between eating species and food host species. For example, as the density of the pathogen population increases the most susceptible host types will be severely attacked. The selective elimination of the susceptible host-types results in an increase in the number of resistant host genotypes and in this way the quality of the food supplied the pathogen population is reduced.

When the concentration of the many resistant genes in the host population reaches a high enough level the pathogen population will decline and be restricted to feeding on interest from the host population. At this stage relative balance will exist between pathogen and host.

Once achieved how will this balance be maintained? Any answer to this is complicated because pathogens reproduce quickly and in great numbers. Increasing resistance in the host will cause increased mortality and selective pressure on the pathogen population. With its comparatively high reproductive rate and short generation time, the pathogen should be capable of overcoming host resistance. Logically this would be disadvantageous to the pathogen, because as it destroys its host and food supply it ultimately destroys itself.

Such destruction seldom occurs in nature, and therefore, some natural phenomenon must prevent the pathogen from evolving and becoming virulent. There are at least two possible conditions under which this balance can be achieved in pathogen-host systems. These conditions which operate interdependently are: (1) the genetic make-up of pathogens is relatively simple compared with their hosts, and (2) the polygenic character of host resistance distributed in space and time controls pathogen evolution and increase.

Pathogens are structurally simple and thus have fewer genes than their more complex hosts. For example, a common virus is estimated to have about 200 genes, whereas a common insect like *Drosophila* is estimated to have about 5,000 genes. This gives the insect host or similarly constructed host organism an advantage because it has more genetic material available to resist the pathogen. This also gives the host real advantage compared with a pathogen based on a gene to gene interaction in the pathogen-host relationship. A two to one or ten to one gene ratio of host gene to pathogen gene number would present a difficult barrier for the pathogen to overcome.

The balanced relationship between pathogen and host is stabilized further by the genetics of the host resistance. Most resistance is polygenic, both in an individual and in a population. Genetic diversity in the individuals which make up the host population helps protect the host from the pathogen in time. For example, assume that a total of 10 genes were involved in resistance for the total host population and that any combination of five resistant genes would effectively limit pathogen attack. Thus, a total of 252 effective five-gene combinations would be present in the host population. With so many possible combinations, the chances are rare that any two hosts standing next to one another would have the same five-gene combination. The distances between hosts of the same genotype would be relatively great and this would hinder the transmission of the particular pathogen genotype which could attack this host. Hence, the distribution of hosts in space and time would, under most conditions, provide sufficient discontinuity to limit the numbers of the pathogen (Amer. Naturalist, 1963).

In addition, natural selection under such conditions would no longer favor the virulent pathogen strain associated with a particular host type. A virulent pathogen with a high reproductive rate would quickly destroy its host and would produce relatively few individual pathogens for transmission during the life of the infection.

If the pathogen evolved to avirulence and limited its feeding only on interest of its host, it would be able to produce more progeny than the virulent type during the life of the infection. This would increase its chance of transmission and survival. This type of evolution is not based on group selection. It is selection for the one individual pathogen which initially starts the colony and infection. Under these conditions the avirulent pathogen genotypes would have greater chances for survival than the virulent types and in time the avirulent type would dominate.

A genetically diverse host population would lead to a genetically diverse pathogen population—specific pathogen genotypes could attack only specific host genotypes. This diversity in the pathogen would help maintain the genetic diversity in the host. In this way, evolution of diversity in the pathogen population would also aid the evolution of balance and stability in the pathogen-host system.

The two possible conditions for maintaining balance in the pathogen-host relationship operate interdependently in nature. These conditions occurring in conjunction with the genetic feed-back mechanism prevent the pathogen from destroying its food supply and thus itself. Balance between pathogen and host has survival value for both and plays an important role in interspecies evolution.

FACTORS AFFECTING THE SUSCEPTIBILITY OF INSECTS TO VIRUSES

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Two broad categories of factors, endogenous and exogenous, affect the susceptibility of insects to viruses. Both types of factors, however, may act together, e.g., when stressors affect latent or chronic virus infections. The endogenous factors are concerned with the insect host and the virus. Insects are generally resistant to viruses which infect other species. However, the cytoplasmic-polyhedrosis viruses have a fairly wide host range; the nuclear-polyhedrosis viruses are more limited, and the granulosis viruses are most restricted, possibly because of insufficient studies. The non-inclusion virus of *Tipula paludosa* has a very wide host range when tested by intrahemocoelic inoculation.

As an insect larva matures, it becomes increasingly resistant to certain virus infections, a case of maturation immunity. Some workers question this generalization and the problem cannot be resolved without quantitative data, such as those obtainable with bioassay. In the sawflies, the prepupal stage with its embryonic midgut cells is immune but the larval, pupal, and adult stages are susceptible to the nuclear-polyhedrosis virus. Until recently, the general opinion has been that lepidopterous adults are immune to active virus infections, even though they may transmit the virus to their offspring in an active or latent state. This supposition is not true in all cases. Antiviral substances are present in the midgut of the silkworm larva (*Bombyx mori*), but have not yet been found in other insect species.

The individuals within an insect population may vary in their susceptibility to virus diseases. The host quality may be important in the maintenance and dissemination of the viruses. Insect populations which exhibit resistance to virus occur under natural conditions. Certain populations which had long association with their viruses may develop resistance.

Insect strains which are resistant to their viruses have been developed under laboratory conditions. The silkworm has strains which differ in their susceptibility to the nuclear and cytoplasmic polyhedroses. In the honey bee the natural resistance exhibited by some colonies to the paralysis and the sacbrood viruses may be hereditary.

The vaccination of the silkworm against the nuclear- and the cytoplasmic-polyhedrosis viruses has been accomplished. The vaccines have been prepared from infected hemolymph, partially purified virus, and heat-inactivated virus.

Virus epizootics tend to occur more frequently at high than at low host densities, but the initiation of the epizootics may occur at low or high densities. The environmental capacity for the insect species is also important in virus epizootics.

The virulence and pathogenicity of the virus are dependent, within certain limits, on dosage or concentration. An increase in the dosage generally results in a decrease in the period of lethal infection. Strains which differ in their virulence and pathogenicity occur in the polyhedrosis viruses. These strains possess characteristic polyhedra with distinct shapes.

Some insect species are susceptible to two or more viruses. The viruses may exist in the insect host in a mutual coexistence or they may react synergistically or interfere with one another. Synergistic associations occur between the granulosis and nuclear-polyhedrosis viruses of *Pseudaletia unipuncta*. Antagonistic reactions between viruses occur in *Bombyx mori*, *Colias eurytheme*, and *Hyphantria cunea*. Thus far, there seems to be no report of the simultaneous infection of the same host cell by two different viruses or strains of a virus.

The virulence of the viruses of *Pieris brassicae* and of *Trichiocampus viminalis* has been increased with passages through susceptible hosts. An increase in temperature increases the virulence and pathogenicity of the virus and results in a shortened period of lethal infection. At high temperatures, however, *Pieris rapae*, *Diprion hercyniae*, *Trichoplusia ni*, *Heliothis zea*, and *Galleria mellonella* develop resistance to virus infections.

The effect of humidity on insect susceptibility to virus diseases is questionable because of conflicting reports. Weather is reported to play some role in the outbreak of virus diseases in the silkworm, *Hyphantria cunea*, and the honey bee. There is some evidence that the host nutrition is important in virus susceptibility. Food quality influences virus mortality in *Bombyx mori*, *Pieris brassicae*, *Malacosoma neustria*, *Porthetria dispar*, and *Galleria mellonella*.

Stress factors affect the insect susceptibility to virus infections. Some endogenous and

many exogenous factors may operate as stressors. Whether the stressors are activating a chronic or a latent virus infection is often difficult to establish. The same stressors are not effective on all insect viruses and in all insect species. A great variety of stressors have been shown to activate the nuclear- and cytoplasmic-polyhedrosis viruses and to a lesser extent the granulosis viruses. The major types of stressors are chemical compounds, nutrients, physical agents, and microorganisms. The microorganisms that activate virus infections are bacteria, granulosis virus, nuclear-polyhedrosis virus, and microsporidia.

BIOCHEMICAL ANALYSIS OF THE EFFECT OF ENVIRONMENTAL FACTORS ON POLYHEDROSIS INDUCTION

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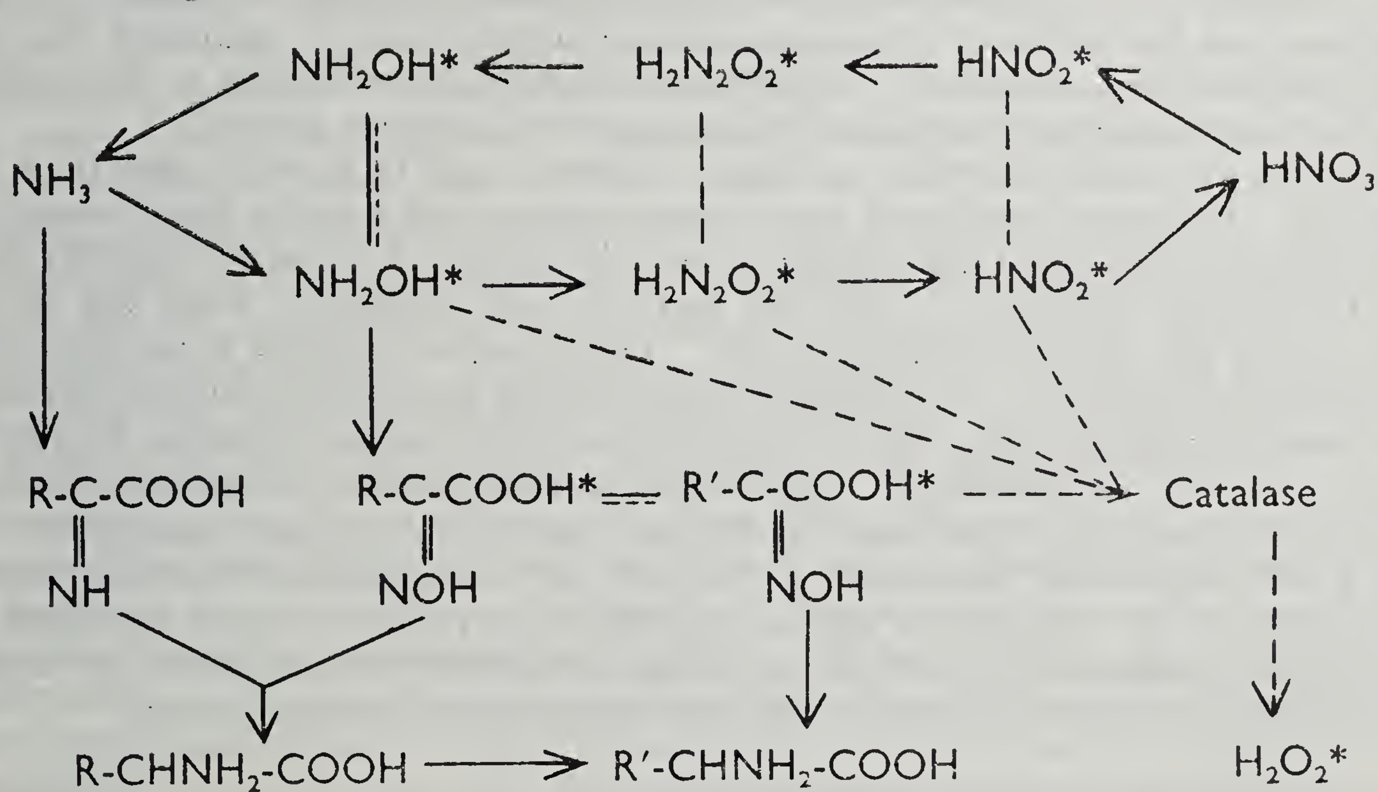
Unfavourable environmental factors, particularly high temperature and excessive cold, induce nuclear viral polyhedrosis. It was found that the inducing treatments, such as heating of *Bombyx mori*-larvae at 45-50°C for 10-15 minutes, cause an increase of oximes and activation of proteases in their tissues. These findings have led to the establishment of a nitrogen cycle which produces virogenic and mutagenic intermediates, and to the demonstration of chromosomal previral genome which contains the genes synthesizing alkaline protease and deoxyribonuclease.

As oxime is formed by the spontaneous combination of hydroxylamine with keto acid, we first sought the way of formation of this amine in the cell. It was proved that hydroxylamine is enzymatically derived from both ammonia and nitric acid even in animal bodies. In the course of these studies, we discovered six new enzymes; ammonium-, hydroxylamine-, hyponitrite- or nitrite dehydrogenase, transoximase and oximase. The oximino group of oximes produced can be transferred to another carbonyl and then reduced to amino acid. It was further observed that the intermediary products of these enzymatic reactions, hydroxylamine, hyponitrite, nitrite and oxime, inhibit cellular catalase without lowering respiration, leading to an accumulation of hydrogen peroxide. We demonstrated that the above four nitrogenous compounds and peroxide have the ability to induce polyhedral virus. Recently, it was witnessed by us and other authors that the five substances just mentioned possess mutagenic action for viruses, bacteria and silkworms. On the basis of those results, I propose now the following scheme.



Yamafuji's cycle producing virogens* and mutagens*.

On the other hand, we found that the metabolic inducers also activate protease and DNase in worm cells. In pursuing this event, it was proved that polyhedral virus contains alkaline proteinase and DNase, and that the genes controlling the synthesis of these enzymes exist in the virus. Further experiments showed that the protease and nuclease of similar nature are present in larval cells, and that cellular chromosomes possess a polyhedral previral genome containing the genes synthesizing these enzymes. Since metabolic processes proceed at the neutral reaction, it is assumed that the genes forming alkaline enzymes might have been produced by a mutation in the past, which had also been caused by the action of mutagenic metabolites. Presumably, the previral genome must be highly resistant and can reduplicate independently. The polyhedral virogenesis, therefore, is formulated as follows:

Cell containing normal chromosomes
↓ Mutation
Cell containing previral genomes
↓ Induction
Cell containing viral particles

THE INFLUENCE OF ENVIRONMENTAL CONDITIONS ON EPIZOOTICS CAUSED BY ENTOMOGENOUS FUNGI

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In nature, fungal epizootics develop only sporadically among insects. Why the incidence of disease should vary from place to place, or from time to time, is not known, but certainly a wide range of factors is involved. Of these weather and climate are of vital importance. Elucidation of the interrelations between entomogenous fungi and their total environment would not only facilitate understanding the mechanism of mycotic infection, but also contribute to the more effective use of these organisms.

Temperature, moisture, and perhaps light, are the more significant components of weather that affect the natural activity of fungal pathogens. Optimum development of most fungi occurs at temperatures between 20 and 30°C., and for about half of them the optimum is between 26 and 30°C. The fluctuating natural environment, duration of exposure to a given temperature, and the influence of non-temperature factors, tend to complicate the relation between temperature and habitat. Entomogenous fungi are world-wide in distribution, so factors other than temperature must also be important in controlling growth.

The effect of relative humidity on fungal epizootics may be more marked than that of temperature. In general, fungi grow best in damp habitats and both the water content of the substrate and the humidity of the atmosphere must be fairly high to permit mycelial development. It has been suggested (1) that the spores of most pathogenic fungi will germinate only in a water film and not in saturated air. The action of humidity is complex and may occur in more than one way. For example, spore-bearing structures are often aerial and thus more exposed to the desiccating effect of the atmosphere than are the vegetative hyphae on the surface of, or within, the substratum. Sporulation, therefore, will not occur on fungus-infected insects that die under dry conditions; such insects merely dry up and disintegrate. Conversely, if rain falls shortly after death of the host, or if conditions are extremely humid, a luxuriant surface mycelial growth and an abundance of conidia may be produced. The composition of the atmosphere, and light including ultraviolet in sublethal doses, are additional factors that have an important effect on the amount and form of fungal growth.

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The routes by which spores are conveyed to the infection site depend largely on external forces (9). Spores liberated at some distance from the ground, as in the case of *Entomophthora aphidis* Hoffman on *Schizolachnus piniradiatae* (Davidson), are distributed at random by air currents and may be carried long distances before settling. Spores so carried are obviously often exposed to unfavorable conditions but the effect that temperature, desiccation, humidity, and light of various types, may have on the viability of such spores during their transit in the air is still largely undetermined (4).

Although climate and weather are important factors, attention must also be given to host population density, spatial distribution, and host migration or activity. Indeed, unusually high populations have often been regarded as the primary factor favoring the development and spread of fungal epizootics (5, 6). In general, fungal pathogens act as imperfectly density-dependent mortality factors (7), i.e., given a suitable temperature and humidity they infect a greater proportion of the insects as the host population increases in density. Antagonism, synergism, and pathogen density are additional factors that affect the development and initiation of epizootics (11, 12). The amount of the initial inoculum has been reported to be as important in fungal outbreaks as any special weather conditions that might prevail (2), but there are few quantitative data on this point.

In general, there is no doubt that many environmental factors, both physical and biotic, play an important role in fungal infection. If a disease is to expand to epizootic proportions, a number of conditions must occur simultaneously: a large population of susceptible insects, a high infective capacity in the pathogen, and optimal environmental conditions for its development. It is not often that all these conditions are synchronized and this may explain the rather infrequent occurrence of fungal epizootics.

During an epizootic, certain insect species in the population complex do not succumb to the disease as readily as others, and some may not succumb at all. Such observations show that there are naturally occurring variations in the susceptibility of insect species. Conversely, it may be argued that mortality differences within and between species are not necessarily due to host differences, but rather to the presence of races or strains of the fungal pathogen, not all of which exhibit the same degree of pathogenicity. Entomogenous fungi have highly developed modes of genetic recombination, and new biotypes are constantly arising by hybridization, by mutation, and by heterokaryosis (8).

Spore dosage may contribute to the wide variation in the infection spectrum. Since there are no quantitative data available, it can only be surmised that a high incidence of infection, or a large fungal outbreak in terms of numbers of hosts infected, is associated with a high concentration of spores. A small dosage, on the other hand, may induce immunity through an inapparent infection, and some insects may not come in contact with spores at all.

Innate immunity is perhaps the most important of the host factors that affect the incidence of disease. The occurrence of acquired immunity whether active or passive in insects still remains an open question. There are indications, however, that protective systems can form in insects under laboratory conditions. These, though they develop rather quickly, are not important or of long duration (10).

The importance of stress as a factor in insect mortality is referred to frequently. The deleterious effects of crowding, tissue damage, under-nutrition, integrated control measures, and particularly the application of sub-lethal doses of insecticides, tend to reduce the tolerance of some pest insects to infection. Environmental conditions that are favorable for the optimum growth of the host population would be expected to increase the resistance of the host, and unfavorable conditions would be expected to enhance the development of disease (3).

In summary, it is evident that insect fungal pathogens, like many other fungi, are extremely dependant for development, survival, and transference, on the complex of conditions that make up the general environment. Temperature, moisture, light, air currents, host population density, host activity, antagonism, synergism, pathogen density, genetic make-up, and stress, are a few of the components known to influence the severity and extent of fungal infection. It is suggested that it is only by increasing our knowledge of the interrelationships between the different environmental agents and the various fungal pathogens, that we shall be able to improve and extend our understanding of the diseases which they cause.

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INFLUENCE OF ENVIRONMENTAL FACTORS ON PROTOZOAN DISEASES OF INSECTS

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Environmental factors affect Protozoan diseases in ways similar to those in which they affect other diseases of insects. Particular examples are as follows:

Temperature. Protozoa can survive temperatures as low as –20°C or as high as 35°C for a long time, especially when they are still in the insect tissues. Temperature has important effects on the rate of development of protozoa and their insect hosts. It can be used, for example, to sterilise insects affected with microsporidia, which sporulate and then cease to multiply at 46 to 48°C. Some diseases seem to be distributed according to climatic conditions. *Nosema serbica*, for example, infects the gypsy moth only in Southern Europe and the subtropics; in Central Europe it is replaced by other species of protozoa.

Several infections occur only in a particular season. *Caudospora simulii* or *Nosema stricklandi*, for instance, multiply in winter; *Plistophora simulii* and *Thelohania* species multiply in summer. The times when the hosts are exposed to infection or when the insects multiply seem unimportant.

Humidity. Most protozoan spores require high humidities to survive. Freezing is harmful because spores are desiccated by it. Water vapour passes through the proteinaceous material which closes the polar opening of the spores.

Environmental factors much affect the transmission of insect protozoa, particularly those infecting fresh-water insects. Oval or spherical spores, particularly those with smooth surfaces, sediment quickly and become distributed in a circular or elliptical zone about the decaying host. Some spores are long or have long appendages, e.g. species of *Bacillidium*, *Mrazekia* and *Caudospora* or *Barrouxia caudata*, and they are carried for long distances by streams. Individuals of a third, recently discovered group of protozoa have a gelatinous layer on their surface which swells, sometimes to increase eightfold the volume of the parasite. Sometimes only the pansporoblasts such as those of *Thelohania asterias*, which infects midges, have this layer. Another species, *Thelohania fibrata*, has it on spores as well, and *T. lairdi* has it on the free spores only. The density of these encapsulated parasites is low so they are carried far by water or become easily attached to the bodies of birds. They are also more readily filtered off in the mouth-parts of filter-feeding insects than ordinary spores. Some protozoa have more protected means of transmission than these. Transovarial transmission or contamination of the insect egg-shell by pathogens are very efficient methods (more than 80% of larvae of *Homeosoma nebulellum* have been found infected in this way in the field when the population density was as low as 1 larva per 20 plants). Another "closed-circuit" method of transmission is via the ovipositor of parasitic hymenoptera, and we have recently shown in our laboratory that these insects sting without laying any eggs about twice as often as when they do lay eggs. Such efficient methods of transmitting protozoa are, however, still much influenced by environmental conditions.

INFLUENCE DE CERTAINS FACTEURS DU MILIEU SUR LA VIRULENCE DE *RICKETTSIELLA MELOLONTHAE* KRIEG.

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Les rickettsies pathogènes pour l'Homme ou les animaux domestiques sont très sensibles aux agents du milieu, de sorte que, pour la plupart d'entre elles, leur transmission n'est possible que par l'intermédiaire d'un vecteur: insecte ou acarien.

Dès les premières études entreprises sur *Rickettsiella melolonthae* Krieg, responsable de la "maladie bleue" chez les larves de Hannetons (*Melolontha* sp.), il est apparu que ce germe présentait des possibilités de résistance aux facteurs d'agression physico-chimiques de beaucoup supérieures à celles manifestées par les autres rickettsies.

Nous avons cherché à préciser les limites de cette résistance par l'étude des facteurs suivants: pH en milieu aqueux, dessiccation, température, antibiotiques, antiseptiques, modalités de conservation dans le sol.

1. Influence du pH en milieu aqueux. Deux gouttes d'hémolymphe de Ver blanc malade dans 10 cc d'eau stérile à pH 7 conservent leur virulence pendant plus de 2 semaines à la température du laboratoire. Il en de même pour des pH de 5,0 à 8,5.

2. Dessiccation et Temperature. Des frottis d'hémolymphe infectée desséchés sur lame ont été placés à différentes températures –20°C, –8°C, +2°C, +20°C, comparativement à d'autres modes de conservation: effilures de pipette Pasteur, cadavres, broyat de larves malades, lyophilisat.

La température a une influence prépondérante sur la conservation du pouvoir pathogène: En frottis, *R. melolonthae* reste infectante après 1 an à +2°C contre moins de 6 mois à 20°C. Elle est encore pathogène après 4 ans à +2°C sous les autres formes de conservation expérimentées.

3. Thermorésistance. Elle est exceptionnellement élevée, car elle peut atteindre 1 heure à 85°C.

4. Antiseptiques.—*Formol gazeux:* des rickettsies, étalées et desséchées sur lame, conservent leur virulence après un séjour de 8 jours dans une enceinte étanche saturée en vapeurs d'aldéhyde formique à 40%. *Formol liquide:* après mélange en parties égales pendant 30 minutes d'aldéhyde formique liquide à 4% avec une suspension purifiée de rickettsies puis lavages rejetés, 4 larves sur les 10 injectées furent infectées. *Alcool:* en adoptant le même protocole expérimental *R. melolonthae* n'est pas détruit par le contact pendant 30 minutes avec l'alcool à 45°C. *Ultraviolets:* après exposition d'un frottis sur lame aux rayons d'une lampe germicide placée à 30 cm au-dessus, pendant une semaine à 20°C, 80 à 90% des Vers blancs injectés meurent de la Rickettsiose.

5. Antibiotiques. Par diverses méthodes, il a été montré que la rickettsie étudiée n'est pas sensible aux antibiotiques usuels et notamment aux tetracyclines, contrairement aux autres germes de ce groupe.

6. Conservation dans le sol. De la terre contaminée par un broyat de larves malades est encore infectante pour des Vers blancs sains après 1 an dans les conditions naturelles.

Ces propriétés très particulières de résistance de *R. melolonthae*, en dehors de leur intérêt en microbiologie comparée, expliquent le mode de transmission de la maladie dans la nature: par conservation dans les cadavres dans le sol et infection par voie per orale des larves saines.

DISEASES OF INSECTS OF MEDICAL IMPORTANCE

MICROSPORIDIA AS PARASITES OF MOSQUITOES

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Twenty-seven species of Microsporidia representing five genera have been described from over forty species of mosquitoes in various parts of the world. These intracellular parasites, particularly the twenty known species of *Thelohania*, are morphologically very similar and were described as new largely on the basis of minute differences in the size and shape of spores. The lack of distinctive characteristics has made it difficult to identify many species and, as a result, identification has usually been strongly influenced by presumed host specificity at either the generic or specific level. Probably more species of Microsporidia, especially *Thelohania*, attack mosquitoes and will be described in the future; such studies, however, must be guided by the use of adequate diagnostic cytological characters, techniques for evaluating host specificity and other distinctive host-parasite relationships. Tissue specificity has been an important diagnostic character for Microsporidia; however, invaded tissues of patently infected mosquitoes are frequently highly modified and difficult to identify.

Members of the genus *Thelohania* have been the most commonly reported microsporidian parasites of mosquitoes. The known species were originally described from larvae with progressive infections and primarily invaded adipose tissue or certain other unidentified tissues which were greatly hypertrophied and occupied the hemocoel. Larvae with such patent infections are easily recognized in the field; they become distended with spores, appear white and usually succumb during the fourth stadium. Fourteen species of mosquitoes infected with *Thelohania* have been studied in California. Observations have been confined to larvae with apparent infections collected in the field, infected larvae reared from egg rafts and a laboratory colony of *Culex tarsalis* in which *T. californica* was transmitted transovarially. By examining serial sections of infected fourth-instar larvae it has been possible to determine relationships between sex, tissue specificity, suppression of sporogony and the expression of

TABLE 1

Sex of patently infected mosquito larvae and tissue specificity of various species of *Thelohania* (Nosematidae), Microsporidia

Host	*Parasite*	*Number Observed Infected* Male	Female	*% Male*	*Tissue Infected*
	Type I				
Aedes squamiger (Coq.)	*Thelohania bolinasae* K. & W.	9	0	100	Oenocyte
A. cataphylla Dyar	*T.* sp.	14	0	100	,,
A. hexodontus Dyar	*T.* sp.	29	0	100	,,
A. ventrovittis Dyar	*T.* sp.	12	0	100	,,
A. increpitus Dyar	*T.* sp.	28	0	100	,,
Culex tarsalis Coq.	*T. californica* K. & L.	43	0	100	,,
C. erythrothorax Dyar	*T. gigantea* K. & W.	12	0	100	,,
	Type II				
A. melanimon Dyar	*T. unica* K. & W.	28	9	76	Oenocyte and Fat
C. apicalis Adams	*T.* sp.	37	4	86	,,
	Type III				
C. thriambus Dyar	*T. noxia* K. & W.	13	15	46	Oenocyte and Fat
A. dorsalis (Meigen)	*T.* sp.	2	2	50	,,
Culiseta incidens (Thom.)	*T. campbelli* K. & W.	22	17	56	Fat
C. inornata (Will.)	*T. inimica* K. & W.	28	25	53	,,
C. particeps (Adams)	*T.* sp.	3	2	60	,,
	Type IV				
C. apicalis Adams	*T. benigna* K. & W.	50	64	44	Fat

patent infections. From these data four basic types of infection have been elucidated (Table I).

It was first established in a laboratory colony of *C. tarsalis* that *T. californica* may be transmitted transovarially and that parasites did not undergo sporogony in female hosts. Laboratory observations indicated that male larvae of *C. tarsalis* usually died during the fourth stadium with progressive infections terminating in massive accumulations of spores which distended the body of the host. Infected female larvae appeared normal, pupated and emerged as apparently healthy adults; they harbored only schizogonic stages of the parasite and laid viable eggs containing mono- and binucleate trophozoites. Oenocyte cells are the sites of infection in *C. tarsalis.*

Observations of infected larvae from field collections indicate that the Type I host-parasite relationship is also experienced by *C. erythrothorax* and all of the univoltine *Aedes* examined (5 species). There is an apparent advantage for the parasite in this type of relationship in univoltine hosts, as the single larval generation each year does not provide opportunity for accumulation of infective spores in a habitat. Selection has provided for survival of female hosts and transovarian transmission, the parasites spending about eleven months of the year as inactive "trophozoites" confined to diapausing mosquito eggs. *C. tarsalis* and *C. erythrothorax*, however, have continuous generations throughout the summer and inactive "trophozoites" overwinter in resting adult female mosquitoes.

The site of invasion in hosts having the Type I infection is the oenocyte. Apparently the ability of female mosquitoes to suppress sporogony and survive normally to transmit infections transovarially is dependent upon having infections limited to this tissue. Moreover, since infected males usually die, an adequate population of healthy males is essential to the establishment of infection.

Data concerning infections in *A. melanimon* and *C. apicalis* indicate a host-parasite relationship similar to that observed in *C. tarsalis.* Both sexes of these two mosquitoes acquire patent infections of certain *Thelohania;* however, 76% of the *A. melanimon* and 86% of the *C. apicalis* examined were males. In this Type II infection there has been an apparent selection for female survival, but it is not known if surviving females suppress sporogony as in the Type I. Patently infected male and female larvae examined in the laboratory harbored dense accumulations of spores; oenocytes and adipose tissue were invaded. Surviving females probably had inapparent infections involving sporogony.

The remaining five species of mosquitoes observed with *Thelohania*, three species of *Culiseta* and one species each of *Aedes* and *Culex*, acquired patent and fatal infections equally in both sexes. Such infections, Type III, were largely confined to adipose tissue, although oenocytes were sometimes involved.

Infected progenies of *Culiseta incidens* and *C. inornata* have been reared from field collected egg rafts and less than 2% of the females survived to the adult stage; it is presumed that these few females were capable of transovarian transmission. Since very few infected females survive, perhaps transovarian transmission is not a major route of infection in this species. Infected egg rafts have been rarely collected in the field; however, over 20% of some larval populations of *C. incidens* have been observed with patent infections, suggesting that *per os* transmission is the more common mode of infection.

A different type of host-parasite relationship has been observed in *C. apicalis* infected with *T. benigna*. Egg rafts of *C. apicalis* infected with *T. benigna* have been collected in the field and resultant progenies have been reared successfully to the adult stage in the laboratory. Larvae had parasites limited to adipose tissue, but invasions were usually restricted to a few small areas which did not interfere with normal larval development or adult survival. Both sexes experience sporogony, survive, and females transmit infections transovarially in this Type IV infection. It is the only example of *Thelohania* infection observed in which sporogony occurred normally and infections typically were not fatal to either sex.

The *per os* tranmission of *Thelohania* in mosquitoes has not been observed in the laboratory or conclusively demonstrated in field tests. Difficulty in demonstrating the transmission of infections by spores makes host specificity particularly difficult to determine.

The influence of the sex of the host on the development of other known microsporidian parasites of mosquitoes has not been studied; however, reports concerning *Plistophora culicis* (Weiser) indicate that it perhaps produces Type IV infections.

INSECT PATHOLOGY AND VECTOR CONTROL: AN INTERNATIONAL COLLABORATIVE PROGRAMME OF RESEARCH

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The purpose of this programme planned by WHO is to foster the development of effective biotic procedures for the control of arthropod vectors of human disease. Its ultimate objective is the designation of highly specific integrated control methodologies on a thoroughly sound ecological basis.

Relevant information is compiled, mimeographed and airmailed to those concerned in the WHO/EBL series of documents. It has a threefold function: to acquaint the Organization's staff, national institutions, etc. with the progress of these and other biological activities relating to environmental health; to distribute to these groups field reports and other communications which would not normally appear in print in WHO publications; and to ensure the early and wide availability of other pertinent data.

Thus, accounts of short-term WHO consultantships, progress reports on current research and manuscripts recently completed by scientists working under other auspices reach those on the mailing list many months before formal publication, and perhaps a year or two before they could learn of the investigations from regular abstracting journals.

It should be mentioned here that an annotated list and bibliography of pathogens, parasites and predators of medically important arthropods, by Dr. D. W. Jenkins, is soon to appear as a *Supplement* to the *Bulletin of the World Health Organization.*

The Organization's encouragement of surveys for natural enemies of arthropod disease vectors began early in 1962. In the first instance, particular attention was paid to the easily-recognised fungal genus *Coelomomyces,* almost all members of which parasitise mosquitoes, and the sporangia of which are often identifiable to the species level in routine slide mounts. Considerable material (comprising new species as well as new locality-and-host records for known species) is now in the hands of a collaborating mycologist, who is now engaged in a comprehensive review of these candidate biological control agents.

During 1964, a laboratory of the United States Dept. of Agric. is receiving WHO support in designing a pocket-sized collecting kit for use in a much more ambitious survey extending to pathogens and parasites of arthropod disease vectors in general. From 1965, an existing laboratory is to be designated as the international reference centre to which all specimens resulting from this survey will be sent for diagnosis. After the rapid provision of a brief interim report to the Environmental Biology Unit, the centre will forward the material itself to one or more collaborating laboratories, for intensive study.

Dr. M. F. Madelin's intensive studies of a Northern Rhodesian *Coelomomyces* at the University of Bristol, and Dr. G. Kovchasov's establishment of a laboratory stock of South American "annual fish" (cyprinodonts, the eggs of which are unusually resistant to drying) for a field assessment of their potentialities against anopheline larvae in temporary pools at Varna, Bulgaria are examples of such work. With regard to field trials, it may be recollected that the research programme under consideration actually began with the 1958 introduction of *Coelomomyces* fungi into the Tokelau Islands, where it was established that the filariasis vector *Aedes polynesiensis* was free from these organisms. By 1960, 13·6 per cent of a sample of 118 container habitats of this mosquito on the atoll in question yielded either diseased larvae or viable sporangia (Laird and Colless, 1962, Proc. XI Internat. Congr. Entomol., 2: 867-8); and at last report, in 1963, larval infections were recorded from 37·1 per cent of a sample of 35 such habitats.

Full attention has also been given to the encouragement of allied research viewed as fundamental to the better understanding and eventual practical use of ecological agents for vector control. In this connection, short-term consultants recruited by the Organization have made field appraisals of the ecology of several insects of public health importance. Other studies and related scientific meetings organised by WHO, have taken place or are in prospect. One such meeting is the symposium on culture procedures for arthropod vectors and their biological control agents held in Florida from 30 September to 4 October 1963; the papers are to be published shortly.

SOME EFFECTS OF THE MOSQUITO HOST ON MALARIAL PARASITES

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Investigations at WRAIR during the past few years have been directed towards an interpretation of mosquito susceptibility in relation to genetic and physiologic factors using a *Plasmodium gallinaceum—Aedes aegypti*—chick system. Our initial study was to determine whether or not susceptibility to infection is under genetic control. If a quantitative character such as malarial oocyst number is under genetic control to some extent, there should be some resemblance between relatives in respect to this trait. Conversely, if this attribute was mainly or wholly under environmental control, there should be little or no correlation between relatives. The relatively high rank correlation coefficient between parents and offspring for oocyst number ($r' = +0{\cdot}46$) indicates that the progeny derived from more susceptible mothers are more susceptible to infection than ones from less susceptible mothers. The higher correlation between parent and offspring as contrasted to that between sisters and offspring ($r' = +0{\cdot}29$) is consistent with a trait under genetic control.

Using a system of genetic selection which tended to alleviate some of the deleterious effects of inbreeding, selection for high and low oocyst count was conducted for thirty generations. Selection for high susceptibility was continued for seven generations and then terminated due to inbreeding effects. Mosquitoes selected for low susceptibility have shown no changes in viability. The asymmetrical nature of the response to selection was apparent. At the end of the selection for high susceptibility, this line was no higher than the control. On the other hand, the line selected for low oocyst count has shown a steady increase downward. There has been an average decrease in susceptibility in the range of 3·5% per generation. Correlated with this decrease in susceptibility, there has been an increase in the number of mosquitoes refractory to infection. This downward trend in the low line continued until the 26th generation when a plateau was reached.

With the presence of mosquitoes with low susceptibility it was possible to make appropriate genetic crosses to determine the genetic mechanism involved. The fact that the F_2, F_3 and F_4 of crosses between susceptible and resistant strains were no more variable than the F_1 and the bimodality exhibited by backcrosses among the susceptible and resistant strains indicated that a single Mendelian factor or a group of closely linked genes was involved. The intermediate values of the F_1 generation of all crosses indicate that incomplete dominance is involved.

It is not expected that this genetic model of mosquito susceptibility is applicable to all mosquito-pathogen relationships, nor even to different malarial host-parasite systems. However, it does illustrate that a complex host-parasite system may be defined in a more analytical manner.

The work of Garnham and Weathersby indicates that the mechanism involved is to be sought within the internal *milieu* of the host. We are in agreement with this and have attempted to demonstrate the presence of a substance associated with a genotype providing a favorable environment for the parasite.

We have altered the susceptibility of mosquitoes to infection by orally administering extracts from susceptible and resistant mosquitoes prior to an infective meal. The extracts were suspended in a sucrose solution and were made available to experimental mosquitoes in lieu of their regular regimen for a four day period. Highly susceptible mosquitoes provided with extracts from resistant females developed significantly fewer oocyst than controls or mosquitoes given the homologous extract. Resistant mosquitoes exposed to extracts from both resistant and susceptible *Aedes aegypti* did not demonstrate any change in susceptibility. Since a change in susceptibility was only unidirectional, it would indicate that there is an inhibitory compound present in the resistant mosquitoes which prevents normal parasite development. We know that the inhibitory compound may be recovered from preparations which have been stored at –20°C for six months and that incubation at 37°C will not diminish its action on plasmodial development.

There has been an associated reduction in the rate of growth of oocysts in the resistant mosquitoes. Mature sporozoites were present in the resistant mosquitoes a day later than in the controls.

THE ROLE AND USE OF NEMATODES IN THE REGULATION AND CONTROL OF INSECTS OF MEDICAL IMPORTANCE

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Nearly 300 records of mermithid parasitism of insects of medical importance are found in the literature. Most of these parasites are recorded from the Culicidae, Simuliidae, and Chironomidae. The taxonomy of the Mermithidae is complex partly because characteristics of sexually mature animals are used and the most commonly encountered forms, the parasitic ones, are immature. More species of mermithids are now known, especially in the parasites of the Simuliidae, and it may be reasonably assumed that in a few years, there will be a much clearer taxonomic picture of these worms. The life cycles of these parasites follow the usual pattern for mermithids. Modifications include oral infection of the host, parasitism of adult insects, and rapid maturation of parasites following emergence. These modifications are adaptations to the life cycle of the host. The emergence of the mermithids kills the host, and in this fact lies the importance of these worms as potential biological control agents. Prior to emergence, the parasite may inhibit histoblast formation, prevent pupation, and in the case of both simuliids, and especially chironomids, cause the host insects to become intersexes.

Mermithids appear reasonably specific in their parasitism of these hosts, especially in the Chironomidae. There are numerous records of percentage parasitism in the literature, and a review of these clearly shows that the mermithids have localized, discontinuous, or contagious distribution throughout the geographical range of the host. In these localized centres they may attain very high rates of parasitism and actually lead to the virtual elimination of the host populations. Both Rubtsov (1950) and Phelps and DeFoliart (1964) have suggested that this may have occurred in certain Russian and Wisconsin rivers. These characteristics, namely, adaptation to the host life cycle, the death of the host upon parasite emergence, reasonably restricted specificity, and high host parasitism suggests that mermithids need consideration as a factor in the natural regulation of populations of insects of medical importance and also that they have a potential as agents for the biological control of these insects.

VIROSES D'INSECTES A IMPORTANCE MEDICALE

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Introduction. Grâce aux recherches de plus en plus intenses, au cours des vingt dernières années, un nombre considérable de maladies à virus a été mis en évidence chez les Arthropodes. Toutefois, peut être en partie, à cause des motifs économiques, ces cas connus sont très inégalement répartis, entre les différents groupes.

Ainsi, la grande majorité des virus d'invertébrés a été décrite chez les Lépidoptères. Quatre types à corps d'inclusion protéiniques et deux sans inclusions attaquent plusieurs centaines d'espèces.

Pour les autres groupes d'insectes, nos connaissances sont réduites. On note chez les Coléoptères (*Melolontha*) une affection sans inclusion (10) et un type ressemblant à ceux de la série de la vaccine (18).

Chez les Orthoptères et les Hémiptères aucune virose n'est connue, tandis que chez les Tenthrèdes (Hyménoptères), on note une polyédrie (3) et chez l'abeille, plusieurs maladies probablement virales, telles que le sacbrood, la paralysie, le mal des forêts (sous presse). Parmi les Diptères, des viroses sans (22) et avec (13, 11) corps d'inclusion ont été observées chez les Tipules, et des cas mal étudiés chez les moustiques et les mouches.

Rares sont les viroses connues chez d'autres invertébrés. Quelques affections chez les acariens paraissent être de cette origine (16, 15).

Les maladies à rickettsies sont représentées chez les Coléoptères (*Popillia*, *Melolontha*) (6, 7, 8, 21), les Diptères (*Tipula*) (12) et les Orthoptères (*Gryllus*) (19).

Ce résumé comparatif montre que ce sont précisément les groupes d'Arthropodes (Diptères, Hémiptères et Acariens) auxquels les vecteurs appartiennent qui sont les moins étudiés du point de vue virologie. Nous essayerons d'analyser les observations en grande partie incomplètes.

Cas pathologiques observes chez les arthropodes vecteurs. Parmi les données existant sur les maladies d'Arthropodes intéressant la médecine, celles concernant les viroses ne permettent pas de dégager des groupes importants comme les polyédries chez les Lépidoptères. Il ne sera donc possible de mentionner que des cas pour lesquels la nature virale a été envisagée ou montrée à des degrés variés.

Ainsi, Del Guercio (1926) a observé dans les larves de *Culex* et d'*Anopheles* des corps rappelant les polyèdres des Lépidoptères et les a dénommé "microbi poliedrici". Toutefois, ni la nature infectieuse, ni la structure de ces éléments ne ressortent des descriptions et il est difficile de considérer d'après ces observations, qu'il s'agit d'une virose.

D'ailleurs, il pourrait s'agir de corps polyédriques dont l'origine non virale a été récemment montrée (2, 17) à certains stades physiologiques, ou au cours de troubles métaboliques. La ressemblance de ces corps avec les polyèdres viraux est souvent telle que certaines descriptions de viroses faites sans examen au microscope électronique sont vraisemblablement erronnées. Des réactions tinctoriales différentielles (2) ou l'examen des coupes au microscope électronique sont nécessaires pour établir une discrimination.

Récemment des corps cubiques de 2 à 3μ ont été remarqués dans les noyaux des cellules de *Culex tarsalis* Coquillett et supposés être les signes d'une virose, car ils ont été trouvés dans les larves affaiblies présentant des points de mélanisation (9). Des études plus approfondies seront nécessaires pour préciser la nature de l'affection.

Chez *Anopheles subpictus* Grassi, des inclusions nucléaires que les auteurs n'assimilent pas aux polyèdres ont été signalées par Dasgupta et Ray (4, 5) dans les cellules secrétrices de l'intestin moyen de la larve. L'observation ayant été faite sur un exemplaire sans possibilité de reproduction, d'autres recherches sont indispensables pour envisager une origine virale.

A ce propos, nous mentionnons l'existence d'inclusions nucléaires, non virales, telles que les cristaux rhomboédriques que renferment les noyaux des cellules intestinales des *Gryllus* sains ou les éléments polyédriques nucléaires dans le tissu adipeux des larves d'Odonates. Une grande prudence est donc à conseiller avant d'associer une inclusion à une action virale.

La lyse du tissu adipeux des larves da *Musca domestica* L. sans corps d'inclusion a été observée récemment (sous presse). La maladie est transmissible par le filtrat L^3 des tissus, mais la conservation de l'agent est limitée et la congélation et nécessaire. La purification et des examens au microscope électronique sont en cours.

Action pathogene des virus transmis sur les tissus des vecteurs. Les Arthropodes vecteurs sont les sièges d'actions virales particulières consistant en un effet nocif qu'exercent sur aux les virus et surtout les rickettsies pathogènes à l'homme.

Ainsi, les cellules intestinales de *Pediculus humanus* De Geer sont non seulement les lieux d'accumulation de *Rickettsia typhi* (Wolbach et Todd) Philip. et *R. prowazekii* Da Rocha, Lima, mais elles subissent des altérations amenant leur détachement. Le renouvellement de ces cellules n'ayant pas lieu, l'action des rickettsies transmises peut être considérée comme pathologique pour le vecteur (20).

Essais d'adaptation interspecifique. Le nombre restreint de maladies virales et le désir de voir s'installer des épizooties naturelles, ou artificielles dans les populations des vecteurs ont suggéré de rechercher des virus pathogènes pour ces insectes, parmi ceux des espèces voisines.

En effet, dans d'autres groupes d'invertébrés, pour les polyédries cytoplasmiques, des actions interspécifiques ont été notées (14) et pour les polyédries nucléaires, à spectres de virulence plus limités, des passages répétés ont adapté à *Galleria mellonella* L. une souche provenant de *Bombyx mori* L. (1). De même la rickettsie de *Gryllus bimaculatus* Geer. atteint non seulement

toutes les espèces de *Gryllus*, mais peut être transmise expérimentalement à *Locusta*, *Gryllotalpa* et au Coléoptère *Melolontha* (sous presse).

C'est dans cette perspective que la transmission de la virose à inclusions courbes de *Tipula paludosa* Meig. a été tentée dans notre Laboratoire sur *Aedes aegypti* L. et sur *Culex pipiens* L. après inoculation.

Un développement lent de la maladie a été obtenu dans les larves avec formation de quelques corps d'inclusion. Les rickettsies de *Gryllus* ont montré des signes d'adaptation aux tissus adipeux des larves de *Culex* (sous presse).

Conclusions. L'ensemble de ces considérations montre que nos connaissances sur les maladies virales des Arthropodes à intérêt médical sont réduites par rapport à celles concernant les autres groupes d'invertébrés. En même temps, plusieurs observations et expériences laissent entrevoir la possibilité de découvrir de telles affections ou d'en transférer d'autres sur les espèces en question.

Les recherches pourront alors avoir des conséquences importantes dans trois voies principales:

—la compréhension du rôle des épizooties virales dans les fluctuations naturelles des populations de vecteurs

—l'emploi des viroses spécifiques dans la lutte microbiologique contre les Arthropodes vecteurs ou parasites

—l'étude de l'influence des virus propres aux vecteurs à l'installation ou à la transmission des germes pathogènes à l'homme.

Pour l'ensemble de ces projets, il est avant tout nécessaire d'organiser des recherches intenses sur le diagnostic et le dépistage des maladies à virus dans ce groupe jusqu'alors négligé.

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INSECT PATHOLOGY: *BACILLUS THURINGIENSIS*

STUDIES ON ENHANCEMENT OF *BACILLUS THURINGIENSIS* VAR. *THURINGIENSIS*

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Bacillus thuringiensis var. *thuringiensis* Berliner has received considerable attention as a control agent against the gypsy moth, *Porthetria dispar* L. In general, field trials have shown that fairly high amounts are needed to produce significant mortality (1, 3, 4). The present study aimed at finding a means of increasing the insecticidal activity of *B. thuringiensis* and thereby allowing the use of lower amounts of material.

Of a number of chemicals tested under laboratory conditions, only 1% boric acid added to various concentrations of a *B. thuringiensis* suspension resulted in larval mortality that was clearly higher than that resulting in larvae feeding on leaves treated with either alone (3). In six tests they used approximately 400 larvae for each treatment. The percent mortality in larvae fed on leaves treated with *B. thuringiensis* alone was 36% while that of larvae feeding on leaves treated with a combination of 1% boric acid and *B. thuringiensis* was 65%. There was no significant difference in mortality between groups of larvae feeding on untreated leaves and those feeding on leaves treated with boric acid.

In 1964, field tests confirmed the results of laboratory experiments. Individual thorn trees, *Crataegus crus-galli* L., infested with third and forth instar larvae were treated by mist-blower. Thuricide 90T with approximately 24×10^9 spores per ml was mixed at the rate of 1 part to three parts of water, with and without 1% boric acid. Effectiveness was assessed by use of cotton drop-nets placed under the trees and by counts of living larvae on branch terminals.

The mortality, as measured by the drop-nets, of larvae feeding on foliage treated with the combination was approximately double that of larvae feeding on trees treated with *B. thuringiensis*. Mortality of larvae in trees treated with 1% boric acid was slightly higher than mortality of those on check trees. Check mortality resulted mainly from attack by parasites.

The effects of the spray were noted within 24 hours and lasted for at least a week. Counts of living larvae on branch terminals tended to parallel results obtained with drop-nets. The reduction was greatest with the combination although in none did it approach 100%.

Further laboratory studies showed that boric acid enhanced the activity of *B. thuringiensis* formulations from two other sources.

In general 1% boric acid exhibited a low level of toxicity to gypsy moth larvae, usually just slightly higher than that of the check. Larvae did not appear to avoid treated foliage and in the field they appeared to develop normally. Planimeter readings in one test in the laboratory showed that the rate of feeding was slightly slower.

Preliminary laboratory tests with late instar larvae of the cabbage looper *Trichoplusia ni* Hübner indicated that there is much less feeding and greater mortality when larvae were fed on cabbage leaves sprayed with the combination. Leaves treated with 1:200 *B. thuringiensis* were completely eaten while less than 50% of the leaf was eaten when they were sprayed with 1:200 *B. thuringiensis* and 1% boric acid. Mortality was also greatly increased by the latter treatment.

Findings indicate that boric acid combined with *B. thuringiensis* does result in increased mortality over that resulting from the additive mortality when the two are used alone. The reasons for this enhancement of activity are under investigation.

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THE SPECIFICITY OF THE PATHOGEN *BACILLUS THURINGIENSIS* VAR. *THURINGIENSIS* BERLINER FOR INSECTS

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Evidence has accumulated during the past few decades to show that at least four toxins are produced by *Bacillus thuringiensis* and its varieties. These substances are (i) The toxic protein crystal, (ii) The so-called "McConnell and Richards toxin" (5) and/or a fly toxin produced by some strains of *Bacillus thuringiensis*, (iii) An enzyme, Phospholipase C, closely related to the *Clostridium perfringens* α-toxin (2), (iv) A group of enzymes or an enzyme, other than Phospholipase C, that attack(s) phospholipids *in vitro*.

Insects from various Orders react to these toxins in several ways. Currently we believe that the Lepidoptera is the only group susceptible to the protein crystal toxin. Most of the species in this order are susceptible although there are a few exceptions.

In certain Lepidoptera the crystal toxin appears to affect the permeability of the gut, allowing the highly alkaline gut contents to penetrate, and change the pH of the blood. The theory that the site of action of the crystal toxin is the cell cementing substance, binding the gut epithelial cells is supported by the discovery that the cell-cementing substance in the wax moth is a mucopolysaccharide composed of glucuronic acid and N-acetyl glucosamine (3). Analysis of the blood of silkworm larvae, fed crystals of *Bacillus thuringiensis* var. *sotto* showed a significant increase in glucosamine in the blood at sixty minutes after ingestion of toxin. This suggests a possible *in vitro* assay method.

An alternative proposal that the toxin affects the membranes of the epithelial cells (4), is not considered feasible since the evidence of change in transport of labelled materials into the blood (55 minutes after toxin ingestion) is not corroborated by previous findings regarding pH changes in the blood (changes beginning 10 minutes after toxin ingestion) and by histological findings, showing complete breakdown of epithelial cells 45 minutes after intake of crystal toxin.

The fly toxin, produced by some of the *B. thuringiensis* var. *thuringiensis* varieties, is apparently marked by the salt, calcium dipicolinate which gives a triple peak of absorbance upon spectrophotometric analysis; the main peak is of 270 milli-microns. This toxin apparently kills only Diptera including *Musca domestica*, *Musca autumnalis* and *Aedes aegypti*.

The possibility of the existence of a second toxin with a peak of absorbance at 258 milli-microns is suspected. This toxin may affect both Diptera and Lepidoptera, thus accounting for the conflicting reports of susceptibility of Lepidoptera feeding on the crude supernatant of *B. thuringiensis* cultures. Apparently the manner of growth may produce different toxic substances.

The fly toxin prevents housefly larvae from pupating when the crude dry supernatant is fed in amounts greater than 2·5 parts per thousand grams of larvae. A combination of spectrophotometric analysis and a simple housefly-larva bioassay has been proposed (1).

Finally these crystal forming bacteria produce at least two enzymes that break down phospholipids. One of these is phospholipase C and the other enzyme while yet undefined, clearly destroys phospholipids and should be investigated as a pathological agent.

All of this evidence suggests that standardizing preparations of *Bacillus thuringiensis* is not a simple problem and possibly should depend on a series of bioassays and *in vitro* tests using at least three species of insects. The silk worm and the housefly are recommended as essential to such testing.

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LES PROCESSUS D'INTOXICATION PAR LA TOXINE DU CRISTAL DE *BACILLUS THURINGIENSIS* BERLINER; ACTION SUR LE MESENTERON DE *PIERIS BRASSICAE* L.

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On sait que l'ingestion de cultures sporulées de *Bacillus thuringiensis* peut entraîner des altérations morphologiques de l'épithélium intestinal chez *Anagasta* (*Ephestia*) *kühniella* Zell., *Pieris rapae L.*, *Bombyx mori L.*, et *Galleria mellonella L.*, (8, 9, 3, 4). La présente étude concerne l'intoxication par sondage oesophagien de chenilles du cinquième âge de *Pieris brassicae* L. à l'aide de cristaux de toxine isolés d'une culture de *B. thuringiensis* sérotype I Berliner (1), dont Martouret et Lecadet (5, 6) ont déjà étudié les processus enzymatiques.

Une dose de 0,5 microgramme de cristaux par gramme d'insecte détermine en trois jours, la mortalité totale des individus traités.

Chez les chenilles fixées 18 à 48 heures après le début de l'intoxication, les examens histologiques permettent de constater que sur 18 individus intoxiqués et examinés, 7 seulement présentent des lésions épithéliales du *mesenteron,* suffisamment graves pour entraîner la mort. On remarque que la proportion des individus à l'épithélium lèsé est bien inférieure aux pourcentages de mortalité obtenus dans les lots de référence.

Etant donné que l'ingestion de toxine abaisse en quelques heures, le pH du chyle du *mesenteron* de *Pieris brassicae* L. d'environ 2 unités (7) il a semblé souhaitable de rechercher si cet abaissement de pH n'était pas à l'origine de la désintégration intestinale.

Pour vérifier cette hypothèse, il a été procédé à des sondages oesophagiens avec 0,01 millilitre d'acide citrique N/10: une faible mortalité a été enregistrée, et le pH du *mesenteron,* s'est abaissé seulement en moyenne de 0,6 unité avec des *maxima* de 2 unités. Cette faible variation s'accompagne d'une réaction de l'épithélium du mésointestin se traduisant selon les individus, par une hyperactivité des cryptes de régénération, une stratification des cellules ou une désorganisation allant jusqu'à la disparition quasi totale de l'épithélium.

On ne peut être que frappé par le fait qu'un abaissement du pH, soit par l'acide citrique, soit par la toxine entraîne des réactions morphologiques assez semblables.

Il est alors permis de se demander, si les désintégrations intestinales observées chez les individus intoxiqués par *B. thuringiensis* et attribuées en général à la toxine du cristal élaboré par cet organisme, ne sont pas en fait que des phénomènes secondaires. A l'appui de cette hypothèse, on peut évoquer les travaux de Heimpel (2) qui ont montré à la suite d'intoxication par *Bacillus cereus* Fr. et Fr. chez *Pristiphora erichsonii* Htg., que certains autres organes et notamment les muscles et le système nerveux pouvaient présenter des symptômes pathologiques.

D'autre part, il a été observé que l'abaissement de pH du milieu intestinal provoqué soit par la toxine bactérienne, soit par l'acide citrique favorise le développement de la flore bactérienne. Cette dernière peut alors jouer un rôle important en favorisant la dégradation des tissus intestinaux selon des processus d'interactions pathologiques, notamment décrits chez les Insectes par Vago (10).

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L'INFECTION MICROBIENNE A *BACILLUS THURINGIENSIS* BERLINER CHEZ *EPHESTIA KÜHNIELLA* ZELL. LIEE A LA PRESENCE DU PARASITE *NEMERITIS CANESCENS* GRAV. (HYM. ICHNEUMONIDAE)

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L' action synergique de blessures cutanées et d'infections cryptogamiques, virales ou bactériennes étudiée par plusieurs auteurs a été démontrée surtout par Vago (1).

Une forme particulière de l'enchaînement de blessures avec l'action de *Bacillus thuringiensis* sérotype 1 Berliner (2) a lieu lorsque l'Hyménoptère *Nemeritis canescens* Grav. introduit avec sa tarière des spores de cette bactérie dans le corps de son hôte *Ephestia kühniella* Zell. au cours de la ponte (3).

D'après nos observations, l'action simultanée de ces deux types parasitaires, microbien et entomophage, provoque une nette augmentation de mortalité de l'hôte, due à une infection bactérienne distincte de l'intoxication classique par ingestion de spores et de cristaux de *B. thuringiensis*. Dans ces conditions, le développement de cette bactérie dans l'hémolymphe devient un facteur primordial. En effet, dans certaines conditions de contamination du milieu par la bactérie, la tarière de *N. canescens* peut s'infecter et jouer le rôle d'agent de dispersion de microbes et de déclenchement de l'épizootie, notamment quand interviennent les facteurs de surpopulation et de superparasitisme fréquents chez cet entomophage. Il est important de noter que le contact du parasite *N. canescens* avec l'hôte infecté par l'injection intrahémocoelienne de 0,01 ml de suspension contenant environ 50 éléments bactériens par individu, entraîne dans certaines proportions, la contamination de la tarière au moment de la ponte et l'infection de l'hôte sain lorsqu'il est parasité à son tour. Nous avons observé des faits semblables avec la bactérie *Serratia marcescens* Bizio; de la même façon que Bucher (4) note des infections à *S. marcescens* et *Proteus mirabilis* Hauser dans des nymphes de *Galleria mellonella* L. parasitées par l'Hyménoptère *Itoplectis conquisitor* Say.

Les examens cliniques, hématologiques et histologiques de l'hôte *E. kühniella* infecté par *B. thuringiensis* au cours du parasitisme par *N. canescens* mettent en évidence plusieurs phases dans le processus pathologique.

La première, physiologique, consiste en une réaction hémocytaire déclenchée par la destruction physique de l'hypoderme et éventuellement d'autres tissus. La deuxième, pathologique, est représentée par la constitution d'un foyer de bactéries par suite de la multiplication de la forme végétative dans l'hémolymphe, après leur introduction par la tarière. La troisième phase est une phase d'altération cellulaire due à l'action de toxines de *B. thuringiensis*, libérée au cours de la multiplication de ce germe. Enfin, la dernière phase est celle de la septicémie qui se développe rapidement et provoque, par sa généralisation, une mortalité dans les premières 24 Heures.

Ainsi, le phénomène analysé apparaît comme un enchaînement d'un acte de parasitisme, d'un phénomène physiologique de blessure, d'une réaction hémocytaire, d'altérations cellulaires et tissulaires et d'une prolifération bactérienne septicémique.

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PATHOGENITÄT EINZELNER STÄMME AUS DER GRUPPE *BACILLUS THURINGIENSIS* FÜR VERSCHIEDENE LEPIDOPTEREN-VERTRÄTER

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In unserer Arbeit haben wir die Wirksamkeit von 12 Hauptvertretern der BT-Gruppe auf 8 verschiedene Lepidopteren-Verträter bei standarden Kultivation- und Bestimmungsmethoden verglichen.

Einzelne Stämme haben wir in Laboratorium-Gärtanks kultiviert, das abgeschleuderte Sporenmaterial durch Lyophilisation getrocknet. Die trockene Puderpreparate haben wir auf ungefär gleiche Sporenanzahl standardisiert. Diese Preparate untersuchten wir in Pulverform gegen 8 Raupenarten aus verschiedenen Lepidopterenfamilien. Wir stellten fest, dass sich betreffende Stämme in ihrer Wirksamkeit gegenseitig in Qualität als auch Quantität unterscheiden. BT var. *entomocidus, subtoxicus, thuringiensis* und *galleriae* zeigten sich als wirksamste. Gleich nach diesen kann man die Stämme *dendrolimus, sotto, alesti* und *anduze*, derer Wirksamkeitsspektrum nicht so weit ist, die aber auf manche Schädlinge sehr gute Virulenz behalten, einreihen. Fast wirkungslos sind die Stämme *bombycis, gelechiae, cazaubon* und *B.*ex *Cicada plebeja.* Die Virulenz der Stämme *galleriae* und *dendrolimus* können wir im Verhältnis zum Wirtsorganismus, aus welchem diese Stämme ursprünglich isoliert wurden, anführen.

Im weiteren Arbeitsabteil versuchten wir Unterschiede in einzelnen Faktoren, die an der Wirkung des *Bacillus thuringiensis* teilnehmen, zu finden. Der wirksamste Bestandteil ist thermolabiles Endotoxin in kristalliner Form, das sich in den Zellen in der Sporulationsphase bildet. Mit Hilfe von elektronischem Mikroskop haben wir die Kristallmolekularstruktur bei 5 der angeführten Stämme studiert und Unterschiede, die mit verschiedener Virulenz der Stämme auf Insekten zusammenhängen könnten, gesucht. Wir stellten fest, dass Eiweissinklusionen aller untersuchten Stämme von bipyramidaler Form mit gefurchter Oberfläche sind. Bei 100-200 tausendmaler Vergrösserung konnten wir auf den Aufnahmen feststellen, dass Kristalle aus Reihen von globulären Formationen bestehen, die das ganze Kristall ausfüllen. Die Anzahl der Globulen in Reihen als auch die Reihenanzahl ist auch im Rahmen eines einzigen Stammes ungleich. Die Durchschnittsgrösse der Globulen ist bei einzelnen Stämmen verschieden.

Bei dem Vergleich angeführter Stämme haben wir auch die Antibiotikaproduktion wirksam gegen Gram-positive Keime beobachtet. Wir stellten fest, dass aus beobachteten Stämmen nicht nur die am meisten virulenten wie BT var. *thuringiensis, subtoxicus* und *entomocidus*, sondern auch weniger virulente *sotto* und fast wirkungslose *gelechiae* wirksames Antibiotikum gegen *Bacillus subtilis* und *Sarcina flava* produzieren. Die Stämme *galleriae, dendrolimus, alesti* und *anduze*, die auch noch zwischen Stämme mit durchschnittlicher Virulenz gezählt werden, keines Antibiotikum unter unseren Bedingungen produzieren.

Ein weiterer Faktor, der der Meinung einiger Autoren nach auch eine Rolle in der Wirkung von Stämmen der BT-Gruppe hat, ist der Proteinasen-Komplex. Wir haben die proteolytische Wirkung angeführter 12 Stämme auf Gelatine verglichen. Alle untersuchten Stämme wiesen Proteolyse vor, am meisten BT var. *alesti, anduze* und *B.* ex *Cicada plebeja*, am wenigsten *galleriae, gelechiae* und *cazaubon.* Wenn auch Bucher (1960) den proteolytischen Enzymen einen grossen Anteil in der Pathogenität zuschreibt, haben wir keine Korrelation zwischen der Proteolyse und Virulenz besagter Stämme gefunden.

Ergebnisse, die wir in unserer Arbeit erzielt haben, ermöglichen uns sich ein Bild über den Charakter einzelner Stämme der BT-Gruppe zu schaffen. Fur praktischen Gebrauch der Preparate weisen diese auf Möglichkeit hin spezifische Stämme gegen gewissen bedeutungsvollen Wirtschaftsschädlingen auszuwählen.

INFLUENCE OF CROWDING AND TEMPERATURE ON SUSCEPTIBILITY OF STORED-PRODUCTS INFESTING MOTHS AGAINST *BACILLUS THURINGIENSIS*

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Facts on environmental factors influencing the susceptibility of insects to pathogens are still scarce. I tried to add something to our knowledge, giving sublethal doses of *Bacillus thuringiensis* (B.T.).

We use plastic boxes with 20 g nutrient (wheat germs and glycerin) and add to it freshly laid eggs of the moths. Experiments were done in constant temperature cells, which also were kept under constant humidity (65% R.H.). The investigations were restricted to the observation of the development time in days and the number of hatched moths.

TABLE I

EFFECT OF THREE DIFFERENT TEMPERATURES ON THE DEVELOPMENT TIME AND MORTALITY OF LARVAE OF CADRA CAUTELLA, TREATED WITH BACILLUS THURINGIENSIS

	Development time in days						Hatched moths					
Treatment:	None		5 mg		20mg		None		5 mg		20mg	
Temperature °C	Time	%	Time	%	Time	%	Nr	%	Nr	%	Nr	%
30	26	100	31	119	36	138	32	100	30	94	24	75
25	38	100	44	116	49	129	32	100	27	84	17	53
20	62	100	72	116	84	135	30	100	23	77	18	60

TABLE II

EFFECT OF CROWDING IN THE FIRST GENERATION ON THE DEVELOPMENT TIME AND MORTALITY OF SECOND GENERATION LARVAE OF CADRA CAUTELLA, TREATED WITH BACILLUS THURINGIENSIS

	Development time in days								Hatched moths							
Treatment:	None		3 mg		6 mg		12 mg		None		3 mg		6 mg		12 mg	
	Time	%	Time	%	Time	%	Time	%	Nr	%	Nr	%	Nr	%	Nr	%
Crowding of 1st generation (eggs per box)																
10	26	100	42	161	41	158	54	208	15	100	15	100	6	40	3	20
50	26	100	52	200	42	161	54	208	15	100	5	33	2	13	3	20
250	26	100	35	135	36	146	51	196	20	100	14	70	3	20	6	30

TABLE III

EFFECT OF CROWDING IN THE FIRST GENERATION ON THE DEVELOPMENT TIME AND MORTALITY OF SECOND GENERATION LARVAE OF PLODIA INTERPUNCTELLA, TREATED WITH BACILLUS-THURINGIENSIS

	Development time in days								Hatched moths							
Treatment:	None		2 mg		5 mg		10mg		None		2 mg		5 mg		10mg	
	Time	%	Time	%	Time	%	Time	%	Nr	%	Nr	%	Nr	%	Nr	%
Crowding of 1st generation (eggs per box)																
10	26	100	34	131	35	135	35	135	18	100	20	111	14	77	7	39
50	26	100	35	135	38	146	38	146	38	100	27	71	16	42	6	16
250	25	100	34	136	35	140	34	136	15	100	14	93	11	73	2	13

Two series of experiments were done:

(1) TEMPERATURE EXPERIMENT: Boxes kept at 30, 25 and 20°C, while 5 mg, 20 mg and none was added of a dust containing B.T. (Bactospeine IP 54-1960, 100 U.B./mg, dust mixture 10% Péchiney, France). The results with the Almond Moth, *Cadra cautella*, are shown in Table I (means of six experiments). No differences between the time of development at different temperatures were found. There was a slight indication that at the lower temperatures a lower percentage of moths were hatching—however, at the lower temperatures the development time was longer, so the larvae were exposed longer to the poison. Comparable results were obtained with the Indian Meal Moth, *Plodia interpunctella*: very slow development at 20°C, and few moths hatching, especially in the treated series. I conclude that no definite influence of temperature is apparent.

(2) CROWDING EXPERIMENTS: A first generation was bred with 10, 50 and 250 eggs per box respectively (50 being a convenient density) at 30°C, and without addition of B.T. The moths that hatched were kept separately, mated and their eggs were used to breed a second generation. Here the density was the same in all boxes, 50 eggs. Temperature was again 30°C, and now three concentrations of B.T. were added. *Cadra cautella* results are shown in Table II (means of 2 experiments). They give an indication which was unexpected: the series, bred on 50-eggs density in both generations, was more susceptible (less moths hatching) than both other series. *Plodia interpunctella* shows in Table III (means of 2 experiments) this phenomenon even more clearly. Under influence of the poison the decrease in hatching percentage is quickest at the 50-eggs series.

I think it is premature at this stage to come to any conclusion: this work is part of our programme to gain knowledge about the fact whether environmental factors induce epidemiological outbreaks in following generations.

CONTRIBUTED PAPERS

SACBROOD OF HONEY BEES

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Sacbrood is a disease of the larval honey bee. Affected larvae die in their prepupal phase after secreting an excess of ecdysial fluid beneath their final unshed larval skin. White (5) obtained evidence that suggested the disease was caused by a virus. Particles about 60 mμ and 30 mμ in diameter have been observed by Steinhaus (4) and Brčák *et al.* (3) respectively in electron microscope preparations of extracts of larvae with sacbrood. We examined similar extracts and found many particles, similar to those described by Brčák *et al.*, about 28 mμ in diameter. About 10^{12} were extracted from each larva. They were purified by alternate cycles of clarification and sedimentation in a high speed centrifuge and then caused sacbrood when added to the food of bee larvae. They closely resemble the particles of acute bee paralysis virus (ABPV) (2, 1) and have the same sedimentation constant (S_{20}) of about 160. However, 10^{10} particles of ABPV added to the food of each of many larvae caused no disease, nor did 10^7 particles of sacbrood virus injected into each of many adult bees cause paralysis, whereas about 10^2 and 10^5 particles respectively of these viruses are sufficient to cause disease in their usual hosts. Moreover the two viruses did not react with each others' antiserum (prepared in rabbits) either in gel-diffusion tests or in precipitin tests in tubes or in infectivity neutralisation tests.

Sacbrood virus isolates from larvae from Switzerland, Canada and five different places in Britain were serologically indistinguishable.

No larvae with sacbrood are found by the end of summer, and extracts of dead larvae that have been dried intact and left for more than a week, are not infective. However, ecdysial fluid, removed from the larvae and dried, retains its infectivity much longer, and it seems possible that the virus overwinters in such dried fluid that is probably spilt on the comb when adult bees remove diseased larvae.

Sacbrood virus is the third non-inclusion forming virus of bees to be identified by electron microscopy, infectivity tests and serology. The others are ABPV and chronic bee paralysis virus (2). Very few other small non-inclusion forming viruses have been found in insects but as three have been identified in the honey bee alone it is likely that very many similar viruses remain to be found in other insects.

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A STUDY OF THE ROLE OF BLOOD CELLS IN INSECT DISEASE

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Insect blood cells are of interest to the insect pathologist for three reasons: they belong to the defense system of the insect body, they can be sites of pathogen multiplication, and they are in the medium through which the pathogen has to travel on its way from one organ to another. The present study uses the blood cell terminology suggested by J. C. Jones (1962, Amer. Zool., 2: 209-46) but the plasmatocytes are subdivided into microplasmatocytes and macroplasmatocytes.

The hemocytes of last-instar armyworms, *Pseudaletia unipuncta* (Haworth), readily phagocytosed injected India ink, latex particles, virus capsules, nuclear polyhedra, killed *Bacillus thuringiensis* Berliner, and, under certain conditions, live *B. thuringiensis.* Excepting heavy doses of the bacteria, the injected materials were usually picked up by the phagocytes within 30 minutes after injection. Phagocytosis was carried out predominantly by the microplasmatocytes, to a lesser extent by macroplasmatocytes and podocytes. This relationship was observed, under varying conditions, in all injected and infected larvae of the armyworm and also in larvae of the wax moth, *Galleria mellonella* (Linnaeus). Spherule cells were never observed to have ingested material. India ink and virus capsules remained in the phagocytes up into the adult stage. India ink can be used to tag the microplasmatocytes and follow their change into adipohemocytes during pupation. The adipohemocytes retain the phagocytic ability. Killed *B. thuringiensis* was digested rapidly by the phagocytes. Live *B. thuringiensis* was digested initially, but the phagocytes began to disintegrate 3 hours after injection of a heavy dose.

Within limits, the percentage of blood cells involved in phagocytosis increased with the amount of material injected. Up to 50 per cent of total circulating cells were capable of phagocytic action.

Injection of inert materials, including virus capsules, hardly affected the differential hemocyte count (DHC) except for heavy doses of latex, which raised the microplasmatocyte count. Heavy doses of killed *B. thuringiensis* raised the microplasmatocyte count and decreased the macroplasmatocyte count. The total hemocyte count (THC) was raised by heavy doses of latex and decreased by heavy doses of killed *B. thuringiensis.* Live *B. thuringiensis* variously affected the DHC and THC, the effect depending upon the dose.

The DHCs of granulosis-diseased armyworms closely approximated those of the controls except for the 6-day period immediately following infection. Diseased larvae do not pupate; consequently, the DHCs did not reflect the changes caused by pupation. During the first six days after infection, the microplasmatocyte count significantly increased whereas the macroplasmatocyte count decreased. A similar change was observed in polyhedrosis-diseased larvae, but it was less pronounced. In both diseases, the percentage of cells that engulfed virus inclusion bodies was surprisingly high—more than 50 per cent of total circulating cells in granulosis-diseased armyworms, and more than 20 per cent of total circulating cells in polyhedrosis-diseased armyworms.

THE SUSCEPTIBILITY OF *THAUMATOPOEA PITYOCAMPA* (SCHIFF.) TO A SPECIFIC POLYHEDRAL VIRUS DISEASE AND TO THE CYTOPLASMIC POLYHEDRAL VIRUS OF *ARCTIA CAJA* (L.)

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Laboratory experiments established that larvae of *Thaumatopoea pityocampa* (Schiff.) are susceptible to a cytoplasmic polyhedrosis virus disease and that the cytoplasmic polyhedrosis virus disease of *Arctia caja* (L.) is also lethal to this species. When *T. pityocampa* were fed with the nuclear polyhedrosis virus of *Neodiprion sertifer* (Geoffr.), *Lymantria* (= *Porthetria*) *dispar* (L.) and the granulosis virus of *Hyphantria cunea* (Drury) and *Pieris brassicae* (L.) they did not develop

a virus disease. The natural polyhedrosis virus of *T. pityocampa* was found to be pathogenic to *A. caja*. The young larvae were shown to be most susceptible to the virus disease and if infected in the later instars some of them pupated and moths emerged. Several of the adult insects were abnormal and their bodies were found to contain large numbers of polyhedra which were pathogenic to either species. The abnormal imagines were able to reproduce and eggs obtained from apparently healthy survivors of the infectivity test gave rise to virus diseased larvae in the next generation.

T. pityocampa is difficult to breed in captivity and it was not possible to obtain fertile eggs and follow the effect of the viruses in the next generation.

The virus polyhedra of *A. caja* was not found to have lost infectivity after storage at 5°C for three years.

Rabbits were used to obtain antiserum and serological tests were carried out. Agglutination and gel-diffusion precipitation tests with both the polyhedra and the virus particles gave a similar reaction and indicated that the viruses of *T. pityocampa* and *A. caja* are closely related.

Field experiments were undertaken and showed that the cytoplasmic polyhedra of *A. caja* as well as the specific polyhedrosis of *T. pityocampa* larvae can be used to control outbreaks of *T. pityocampa* in the natural conditions. Infested pine trees in Istria were sprayed with suspensions of polyhedra when the *T. pityocampa* larvae were in the third instar, September 1961. On examining the trees eight weeks later about 50% of the larvae were found to have been killed with a virus disease and the larvae which remained had ceased to feed because they were also affected by the virus disease. Larvae on unsprayed trees in a nearby plot were found to be healthy and to have severely defoliated the pine trees. Grison and Vago (1959) have shown that the naturally occurring polyhedrosis of *T. pityocampa* can be successfully used to control this pest but the production of virus polyhedra is made difficult by the urticating hairs of the larvae and the problems is breeding this species. *A. caja* is an excellent laboratory insect with several generations in a year and from which the virus polyhedra may be extracted with less danger to the operator.

OBSERVATIONS ON CULTURES OF *PIERIS BRASSICAE* L. SUSCEPTIBLE AND RESISTANT TO GRANULOSIS VIRUS DISEASE

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An attempt has previously been made to show that a culture of *Pieris brassicae* can develop resistance to the granulosis virus disease (1). The present paper gives further evidence on this subject and reports some experiments on the transovarial transmission of this disease.

Three cultures of *P. brassicae* have been used. The Cambridge stock (now in laboratory culture for 14 years), a so called virus free stock and a culture of *P. brassicae* race *cheiranthi* from the Canary Islands. The virus free stock was derived from the culture which was originally compared with the Cambridge culture and found to be more susceptible to the virus. The selection was carried out by breeding from the females showing the least virus among their progeny and by stressing the stock with potassium fluoride. The last virus death occurred in the 16th generation and there have been no virus deaths up to the 30th generation. Other attempts to stress the larvae by crowding, heat, cold and chemicals have failed to produce virus deaths. We conclude, therefore, that the stock is free from virus or carrying it in a latent form which never gives rise to overt disease and cannot be brought out by any of the normal methods.

The susceptible *cheiranthi* stock had only been in the laboratory for three to five generations at the time of the experiments. It was reared under what were conceived to be conditions of low stress. That is to say in small groups of less than 10 larvae, on growing nasturtium plants (which are the natural food of the larvae in the Canary Islands) and in ventilated cages. Other groups reared on cut foliage in jam jars or on cabbage plants showed more virus. In

fact a stock maintained throughout on cabbage was lost due to the high percentage of larvae dying of virus and other causes.

When the resistance of these three stocks to the granulosis was compared it was found that the *cheiranthi* larvae were considerably less resistant than the virus free larvae to virus derived from both the *cheiranthi* stock and from the virus free stock. The virus free larvae were, in turn, less resistant than the larvae of the Cambridge stock. When the viruses from the two stocks were compared at approximately equal concentrations and at three serial dilutions no significant difference was detected between the virulence of the two. In the case of the wattle bagworm (*Kotochalia junodi* Heylaerts) virus obtained from insects 200 miles away was more virulent to the local bagworms than their own virus (2).

It is known that granulosis is transmitted transovarially and that sometimes a very high percentage of larvae die from virus acquired in this way. We have tried to get a high rate of transmission by feeding virus to the larvae of various instars and breeding from the survivors. Using the virus free stock and virus derived from them in the F 1 generation, only 3 larvae out of 1299 bred died of virus and in the F_2 none out of 800 bred died. Using the same stock and virus derived from the F 1 *cheiranthi* stock the rate of transmission was equally low or lower. Perhaps it is only in the more susceptible stocks that the gonads become infected but we have not yet been able to test this suggestion.

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INCONSISTENCY IN THE VECTOR RELATIONS OF THE CITRUS TRISTEZA VIRUS

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Introduction. In a survey of the aphid population of citrus trees in Israel, 3 species were found actually to breed, though to varying extents, on this hostplant. These are *Toxoptera aurantii* (B.d.F.), *Aphis gossypii* Glover, and *Myzus persicae* (Sulzer); the first species being the most abundant one, judging from the round-the-year picture. All these 3 aphids were reported as vectors of the tristeza virus, respectively, in Florida (1), California (2), and India (3)

Since the tristeza virus has been introduced into Israel, most probably by means of infected scionwood, it was deemed imperative to test each one of these 3 aphids as possible vectors of tristeza in Israel. *Aphis pomi* de Geer, which normally does not occur on citrus, was also included in this extensive series of tests, owing to its taxonomic closeness to *Aphis spiraecola* Patch, which is responsible for the natural spread of tristeza in Florida (1).

Methods. In order to ensure maximum comparability with results obtained in the above-mentioned countries, the techniques and procedures followed in our aphid transmission trials were as far as possible identical to those used by each one of the respective workers who achieved positive results with the aphid species concerned.

Results. Following repeated attempts it was not possible, even in a single case, to obtain any aphid transmission of the virus. Results were negative in spite of the fact that the numbers of aphids employed were as high as 700 individuals per test plant (Key lime, or Egyptian sour lime) for *M. persicae;* 1000—for *A. gossypii;* 1500—for *T. aurantii*, and 3000—for *A. pomi.* Incidentally, the clone of *A. gossypii* used in these tests could be readily rotated in both directions between cotton, citrus and marrow plants without any apparent loss of viability.

Discussion. This is not the first instance whereby the same aphid species behaves inconsistently as regards transmissibility of tristeza (see Table 1, which is based on the Conspectus of Kennedy *et al.* (4), and on other sources). Some of these incongruencies in aphid transmissibility among the various countries may be well explained by the existence of different

strains of the virus on the one hand, and different clones or subspecies of aphids on the other. However, in some instances such an explanation proves inadequate. A suggestion is therefore being made to the effect that the particular behaviour of the aphid tested plays a decisive role in determining whether this intricate process of acquisition and inoculation of this apparently stylet-borne virus (5) will be accomplished successfully in one country, or fail in another. It should, however, be borne in mind that we are dealing here with aphids which are not the primary and efficient vectors of this virus, but rather secondary and most inefficient ones. Their behaviour during transmission is greatly dependent on the ecological conditions of the habitat, which are naturally characteristic of each geographical region concerned.
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Table 1
Vector relations of the tristeza virus in different countries

	Toxoptera aurantii	*Myzus persicae*	*Aphis gossypii*	*Aphis spiraecola*	*Toxoptera citricidus*
Brazil	–	–	–	NT	+
California	–	–	+	–	NP
Florida	+	NT	+	+	NP
India	NT	+	+	NP	+
Israel	–	–	–	NP	NP
Texas	NT	NT	–	–	NP

+ Vector NT = no test reported
– Non-vector NP = aphid not present

HYPOPROTEINEMIA IN A NOCTUID LARVA DURING THE COURSE OF NUCLEOPOLYHEDROSIS

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Symptoms and signs of viral disease reflect the changes in structures and functions occurring in the sites of viral replication and maturation. Since in larvae of Lepidoptera the fat body appears to be the main site of blood-protein synthesis, a study of blood plasma proteins in the course of nucleopolyhedrosis may provide information on the type and severity of certain functional lesions in larvae suffering from this viral disease. The fat body of Lepidoptera is one of the main target tissues of nucleopolyhedrosis virus, along with the tracheal matrix and the epidermis. Our studies avoided the late lytic phase of nucleopolyhedrosis: the blood analyses were made during the incubation and prodromal stages of the disease, before the release of viral inclusion bodies into the blood of the sick insects.

Larvae of *Peridroma saucia* (Hübner), the variegated cutworm, were used throughout this study. They were inoculated *per os* with viral inclusion bodies. At varying intervals following inoculation, blood samples of approximately 100 microliters were obtained from each larva. The specific gravity of whole, freshly drawn blood was determined by standard copper sulfate solutions. The refractive index of the blood plasma was measured with a Goldberg-Wolf refractometer. The protein concentration was estimated by ultraviolet absorptiometry at

260 and 280 millimicrons and colorimetrically, with Gornall's biuret reagent, at 540 millimicrons.

The specific-gravity determinations as well as the refractometric data indicate that disease progress is associated with a significant deficit in total solids in the blood of diseased larvae. This deficit is particularly evident in the females, since last-instar healthy female larvae of *P. saucia* (and of other Lepidoptera) accumulate in their blood a higher amount of total solids than males. The results of total plasma protein determinations indicate that there is a significant correlation between refractive index and total protein in the blood plasma of larvae of *P. saucia.* Thus, a statistically reliable estimate of total plasma proteins may be made from the refractive index of the plasma. The deficit in total solids in the blood plasma of larvae of *P. saucia* during the course of nucleopolyhedrosis is larger than that observed after partial food deprivation.

The data presented indicate that hypoproteinemia is definitely a part of the nucleopolyhedrosis syndrome in larvae of *P. saucia* and possibly, because of the role of the fat body in blood-protein synthesis, of other Lepidoptera. We have observed repeatedly that hypoproteinemia is most pronounced when the severity of cytopathic changes in the fat body is greatest. Thus the refractive index of the blood plasma has not only a diagnostic value but, at least in the case of larvae of *P. saucia,* it may also serve to quantify the extent of the lesions in one of the target tissues.

The simplicity and reliability of refractometric determinations using a temperature-compensated Goldberg-Wolf hand refractometer offers the possibility of rapid detection of dysproteinemias for routine diagnostic purposes and epizootiological surveys.

(The full text, tables, and illustrations will be published in vol. 6, no. 4 of the Journal of Insect Pathology.)

PROSPECTS OF INTEGRATED RADIATION AND MICROBIAL CONTROL OF HARMFUL INSECTS

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While taking up this topic our attention is directed first of all to the research into the possible application of the radiation sterilizing method of population suppression. These exploratory investigations have shown that ionizing radiation will induce sterility but there is considerable variation in amounts needed (1). The research also suggests that radiation damage may in some cases prevent application of the method to some insects. In nature some insects appear to be so abundant that the use of sterile male technique may not be feasible without first processing the geographically isolated and non-isolated infested area with other control measures to bring wild population within reach. Such a situation can be tackled from two angles. Firstly, the population may be controlled by means of well tried viruses, bacteria and suitable protozoan such as Microsporidian and Coccidian parasites. Secondly, the release of sterile male insects carrying parasites or pathogens, in order to contaminate the environment and destroy the progeny, has the potential future. In such a situation intensified search has to be made for those pathogens that are non-virulent when present in or on the adult, but are highly virulent to the larvae. *Coelomomyces* and *Thelohania* are probably of this category (2).

A new approach in the form of susceptibility of irradiated insects to pathogens is opening a new field of investigation. The life span of *Tribolium castaneum* and *Tribolium confusum* beetles was shortened considerably when the test insects received *Bacillus thuringiensis* immediately and after an interval of 24 and 144 hours following exposure to 1000 r, 10,000 r, 30,000 r, 50,000 r and 90,000 r doses of X-rays, respectively. The life span of the irradiated beetles was somewhat shortened by the presence of *Farinocystis tribolii*, *Nosema whitei* and *Adelina tribolii*

protozoan parasites in the fat body of the test insects (3).

There are promising prospects of evolving new strains of pathogens of high virulence. Strains of increased virulence of *Beauveria bassiana* and *Aspergillus flavus* have been evolved by means of ionizing radiation (4).

The use of radiation source as an insect repellent and the behavioral aspects of radiation on insects is a fascinating field of future investigation. The water flea, *Daphnia magna* dive from a position near the surface to the bottom of an aquarium when exposed to X-rays (5). Rat fleas have been found to have deserted irradiated rats. The grain beetles are found to aggregate at the side of the container facing away from the source following exposure to high radiation intensities. *Tribolium castaneum* and *Tribolium confusum* beetles aggregate in a corner of the container following exposure to low doses of X-rays (3).

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INTESTINAL MICROORGANISMS OF THE COCKROACH WITH AND WITHOUT INTRACELLULAR SYMBIOTES

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In connection with studies on the biochemical interrelationships between *Blattella germanica* (L.) and its intracellular bacteria (1, 2), a third factor, the intestinal microflora became a matter of concern. Since microbial activity may greatly affect nutritional requirements and metabolic studies in general, a semi-quantitative determination of gut bacteria was undertaken. The insects were surface-sterilized and homogenized and the bacteria were plated out on nutrient agar following serial dilution of the homogenate. Since aureomycin (chlortetracycline) is routinely used in the author's laboratory to eliminate the bacterial symbiotes from the German cockroach, analyses were made not only of untreated cockroaches but also of cockroaches feeding on 0·1 per cent aureomycin and of their aposymbiotic progeny.

The antibiotic virtually eliminated intestinal bacteria within a 48 hour period. However, continued feeding of aureomycin did not suppress microbial growth indefinitely. Aureomycin-resistant species of bacteria began to flourish in some of the insects after several days.

Initial experiments gave indications of a much greater number of intestinal bacteria in cockroaches without intracellular symbiotes. This observation could not be confirmed in more recent studies. At most, it may be stated now that the numbers of gut bacteria in the aposymbiotic cockroach are more variable than in the normal insect.

Since elimination of the intracellular symbiotes results in several metabolic aberrations, it was felt that the aposymbiotic insect might be more susceptible to invasion by one or more bacterial species which, under normal conditions, are non-pathogenic to the cockroach. Therefore, attempts were made to induce a generalized infection by feeding massive quantities of bacteria including known entomophagous types. The following species were used: *Serratia marcescens* Bizio, *Pseudomonas aeruginosa* (Schroeter), *Aerobacter aerogenes* (Kruse), *Bacillus lentimoribus* Dutky, *B. cereus* Frankland and Frankland, *B. alvei* Cheshire and Cheyne, *B. thuringiensis* Berliner.

Neither the aposymbiotic nor the normal insects were visibly affected by the bacteria during a 6 week period following initiation of feeding.

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NEMATODES ASSOCIATED WITH THE PSYCHODIDAE AND OTHER TERRESTRIAL NEMATOCEROUS DIPTERA

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During the past year, several interesting relationships between nematodes and several families of nematocerous Diptera were investigated.

Phoretic associations between Rhabditid nematodes and adult *Psychoda* sp. (Psychodidae) and *Smittia* sp. (Chironomidae) were discovered. These involved the nematodes wrapping themselves around the abdomen in the case of *Psychoda* or wedging themselves in the intersegmental areas of the abdomen in the case of *Smittia*.

Parasitic relationships that were investigated were: (1) An internal parasite found in the abdomen of Psychoda, (2) an undescribed species of *Neoaplectana* parasitizing Sciarid larvae, (3) an undescribed mermithid parasitizing larvae of *Smittia* sp. and *Bradysia* sp. (Mycetophilidae) and a species of *Tripius* found parasitizing the larvae of *Bradysia* sp.

Because of its interesting development, further studies were conducted on the life history of *Tripius*.

A detailed study was made on the penetration of the nematode into its insect host. The penetration was performed with a combination of spear action and flow of enzymatic material which appeared to soften the insect cuticle.

Once inside the host, the females increase greatly in size and the uterine cells enlarge to such an extent, that they are forced out through the vulvar opening of the nematode.

Egg laying continues until the body cavity of the parasitized larva is completely full of eggs and larval nematodes.

The fly larva usually dies before pupation and the nematodes leave the body cavity, mate and the females then seek a new host.

Experiments are now being conducted to determine if the nematode may have potential as a biological control agent, since besides killing most of the larvae, the few parasitized individuals which manage to reach the adult stage are usually sterile.

DESTRUXIN B, AN INSECTICIDAL METABOLITE OF *OOSPORA DESTRUCTOR*

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Isolation. Oospora destructor, a pathogenic fungus of silkworms, was grown in stationary culture at 26 to 28°C for 15 to 18 days on Czapek-Dox medium containing 0·5% peptone. The culture filtrate was treated with charcoal and the insecticidal principles were eluted from the charcoal with n-BuOH-H_2O (1:1, v/v). The butanol phase was concentrated to a syrup, which was thoroughly extracted with benzene. The benzene solution was applied to a neutral alumina column, and this was developed with benzene containing 5 and 10% ethyl acetate to yield destruxins B and A (DB and DA) successively. Recrystallization of DA and DB from benzene—ligroin gave colorless crystals melting at 125°C and 234°C respectively. The yield was 13 to 15 mg. per litre of culture broth for each compound.

Biological Activities. A. *Toxicity to Silkworms.*—Aqueous solutions of DA or DB in serial dilutions were injected into larvae of fifth instar. The minimum amount of the compound required to cause immediate paralysis followed by death was 0·3γ per g. body weight for both DA and DB. However, they showed no activity as stomach or contact poison.

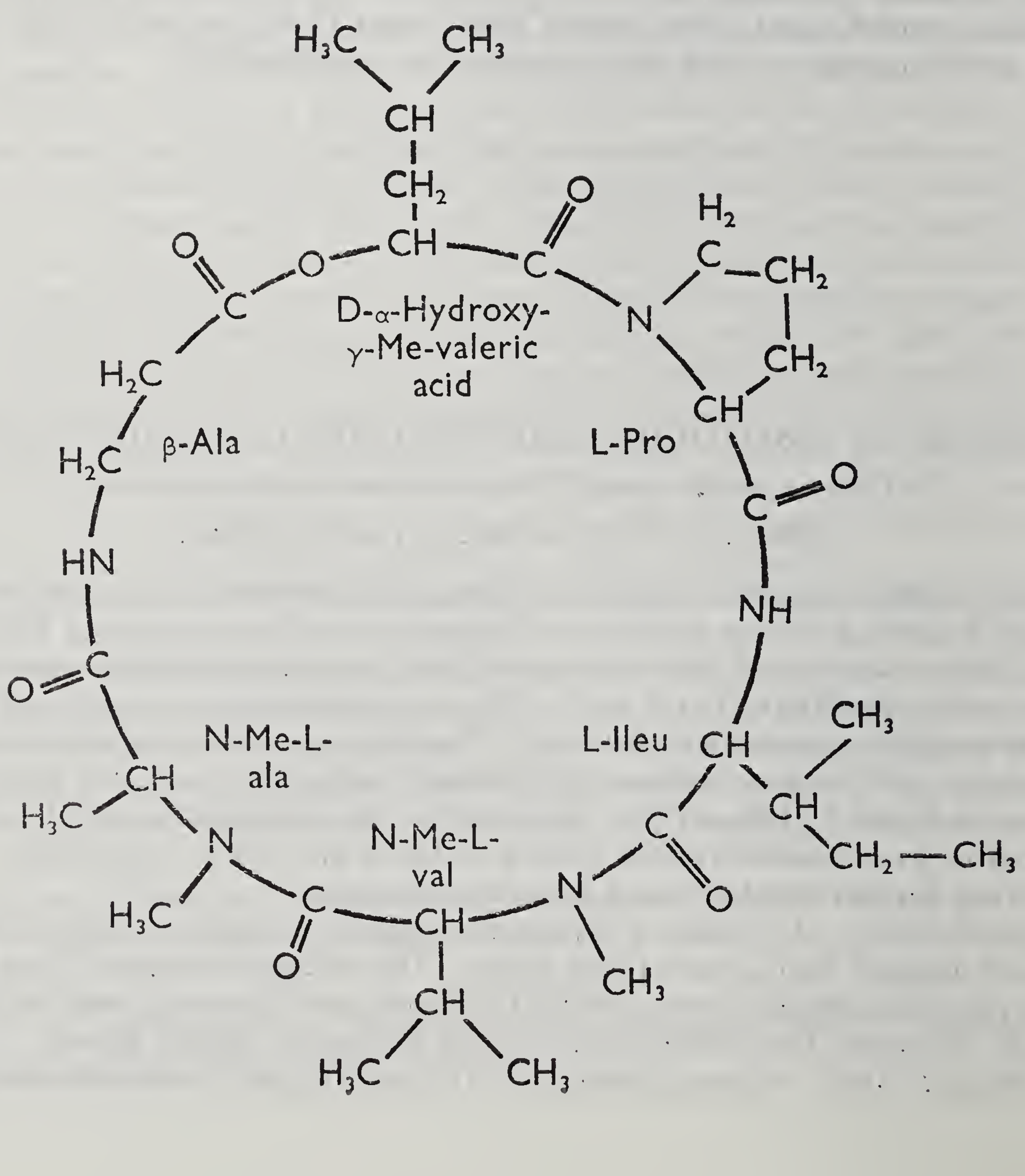
B. *Toxicity to Mice.* Aqueous solutions of DA and DB were intraperitoneally adminis-

tered into mice. In this case DA was far more toxic than was DB, and the minimum amounts of these compounds to cause immediate convulsions on mice followed by death were 1·8 and 17·0 mg. per kg. body weight respectively.

C. *Antimicrobial Activity.* DA and DB were tested by the agar diffusion procedure at a concentration of 500 ppm against a variety of bacteria, fungi and yeasts, but no antimicrobial activity was observed with these compounds.

Chemical Structure. DB is a neutral compound having the molecular formula $C_{30}H_{51}O_7N_5$. $(\alpha)^{23}_{D}$ $-228{\cdot}0°$ (c 0·5, in MeOH). It is easily soluble in alcohols, chloroform, ethyl acetate and benzene, fairly soluble in ether and sparingly soluble in ligroin and water. Its IR spectrum indicates the presence of ester (1732 cm^{-1}) and amide (1690, 1660, 1635 cm^{-1}) functions.

When DB was treated with dilute MeOH-NaOH at 37°C for 48 hrs., its ester linkage was cleft to afford destruxinic acid B(D-acid B). On vigorous hydrolysis with 6N HCl at 120°C for 24 hrs., both DB and D-acid B gave D-α-hydroxy-γ-methylvaleric acid and five amino acids, L-proline, L-isoleucine, N-methyl-L-valine, N-methyl-L-alanine, and β-alanine in equimolar ratios. Hydrazinolysis of D-acid B afforded β-alanine indicating that DB must be a cyclic depsipeptide in which β-alanine forms ester linkage with the hydroxy acid. Partial hydrolysis of DB with conc. HCl at 37°C for five days yielded three major peptides. Then the constitution and sequence of amino acids were determined for each peptide. Based on these experiments DB has been assigned the structure, cyclo-D-α-hydroxy-γ-methylvaleryl-L-prolyl-L-isoleucyl-N-methyl-L-valyl-N-methyl-L-alanyl-β-alanyl. The elucidation of the structure of DA is now in progress.



STUDY ON THE ENTOMOPHTHOROSIS OF APHIDIDAE FOR THEIR PRACTICAL UTILIZATION

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The important role of entomophthorous fungi in the natural control of some insect pests, especially Aphididae, has been ascertained by Grobler (1962), Fluke (1929), Harper (1958), MacLeod (1955) and others. The investigation of entomophthoroses in aphids which attacked leguminous crops in the U.S.S.R. began in 1963. The occurrence of entomophthorous fungi throughout the country has been studied by us. The mortality of pea aphid in some regions of Central Russia has approached 50 per cent. The epizootics were especially heavy in a high population density of the host. The mortality of egg-laying females, up to 30 per cent, reducing the overwintering population, was observed in the Leningrad Region.

Such data should be taken into consideration for pest population forecasting. For this purpose, it is possible to collect living aphids from nature and to observe the incidence of the disease.

Entomophthora aphidis, *E. thaxteriana* and *E. sphaerosperma* are the main causative agents of entomophthoroses in the aphids. Individuals affected by two pathogens can be found. The diagnostic signs have been found for identifying entomophthoroses caused by different pathogens under field conditions. Aphids affected by *E. aphidis* and *E. sphaerosperma* are attached to the substrate with rhizoids. Aphids affected by *E. thaxteriana* are attached by their proboscides. The covering is more obvious in the two former cases. The conidiophores of *E. thaxteriana* project slightly from the body. *E. aphidis* is the most widespread species, however *E. thaxteriana* was found to be more important in autumn in late pea crops, Leningrad Region. It is possible that the individuals affected by *E. aphidis* remain on the plants in greater proportion because they are attached to them by rhizoids. This was also noted by Rockwood (1950).

Attempts to isolate the pathogen fungi into culture revealed the great importance of the composition, and especially the consistence, of the cultural medium. *E. thaxteriana* has been cultivated on semi-liquid Sabourau-dextrose-agar with a drop of sterile water. Two forms of the fungus were isolated; one from the pea aphid, *Acyrthosiphon pisum* Harris, and the other—from the green peach aphid, *Myzodes persicae* Sulz. They differ somewhat in the size of conidia. So far *E. aphidis* has failed to be isolated.

The isolation of *E. thaxteriana* into pure culture enabled us to study the influence of temperature, humidity, light and pH on its growth and sporulation. The mass discharge of conidia has been found to occur only in light, and their germination is possible only at the dew point. The data explain the course of epizootics under natural conditions.

The germination of resting spores of *E. sphaerosperma* collected from dead insects has been studied by us. The resting spores are known to germinate very poorly under laboratory conditions (Hall and Halfhill, 1959). Exposure to various temperatures and humidities did not cause any germination of the resting spores. Germination has been obtained by exposure to X-rays at 1000 r, and the dose rate at 416 r per minute. Exposure to X-rays of other doses as well as gamma rays have been tested, but did not show any effect.

OBSERVATIONS ON THE ASSOCIATION BETWEEN *BRADYNEMA* SP. (NEMATODA: ALLANTONEMATIDAE) AND THE MUSHROOM INFESTING FLY *MEGASELIA HALTERATA* (DIPTERA: PHORIDAE)

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Adult *Megaselia halterata* Wood collected near mushroom farms are frequently parasitized by an eelworm *Bradynema* sp. (Hussey and Wyatt, 1958). *M. halterata* is an important pest of mushrooms as the larvae destroy the mycelium and, if present in sufficient numbers, may prevent the vegetative hyphae colonizing the compost so causing almost complete crop failure. Even where the larval populations are not large enough to reduce the crop the adult flies are a serious nuisance to pickers. As the mushroom crop is grown on sterilized compost insect pests have no natural enemies excepting those introduced by the flies themselves. The only mortality factor known to affect *M. halterata* is this parasitic eelworm.

Bradynema larvae are liberated by female *Megaselia* in groups of 20-40, into the compost during, or shortly after, the act of oviposition. Eelworms do not escape from the female hosts in any other way in life, or death, and are apparently unable to leave the male host under any circumstances. Fertilisation of *Bradynema* females occurs in the third larval stage. They then penetrate the cuticle of first or second instar host larvae and mature within the haemocoele at about the time of eclosion of the host fly from the pupae. Multiparasitism is common, as many as 18 *Bradynema* larvae maturing in one phorid larva. Parasitized males are largely unaffected by the eelworm although some cases of impotence have been found but the average fecundity of parasitized female *M. halterata* is reduced from 50-60 eggs to between 0-6.

Experiments were done to study the effects of host and parasite density on the proportion of the population parasitized by *Bradynema*. Different numbers of parasitized and clean, mated female *M. halterata* were enclosed over different volumes of spawned compost. Between 2 and 25 females, over a range of ratios of parasitized to clean flies from 1:5 to 1:15 were allowed to oviposit in 20, 60, 180 or 3600 g. of compost. The two variables most likely to effect the pattern of parasitization are (i) the density of host larvae and (ii) the number of searching eelworms. The latter cannot be estimated accurately but can be practically expressed by the density of parasitized ovipositing flies. The data showed that, at any given density of parasitized flies, the proportion of phorid larvae parasitized decreased with the increasing larval density. This result can be explained on the assumption that, although eelworm movement in the compost is limited, there is an attractive mechanism guiding the parasites to the nearest host. Even when multiparasitism occurs groups of eelworms in any volume of compost parasitize only the nearest larvae. The most important factor limiting parasitization of the larval population is therefore the density of parasitized females ovipositing in the compost. Since a mushroom crop can support only one, or at the most two, generations of *M. halterata* the opportunity for natural increase in the level of parasitism within a single crop is limited. However the reduction in reproductive potential in a heavily infested population by as much as five times suggests that it may be worth considering measures to increase the proportion of flies parasitized throughout the mushroom farm especially early in the "fly season". Practical considerations probably limit the method to release of parasitized individuals.

Section 12.—MEDICAL AND VETERINARY ENTOMOLOGY

FLIGHT RANGE AND FEEDING HABITS OF BLOOD-SUCKING INSECTS

FLIGHT RANGE AND FEEDING HABITS OF *PHLEBOTOMUS ORIENTALIS* (PSYCHODIDAE, DIPTERA)

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Field studies in south-central Sudan during 1962-63 revealed the following information about the habits of *Phelbotomus orientalis*:

(1) Adults readily fly 300 metres and a flight of 730 metres in 24 hours was recorded.
(2) *P. orientalis* and other sandflies fly at least 2 meters above ground in what are probably long, sustained flights.
(3) Winds below 1·5 m/sec. do not influence biting activity, but between 1·5-2·5 m/sec. activity is diminished and ceases almost entirely above 4·0 m/sec.
(4) Maximum biting activity begins at dusk and continues for the following several hours, the more abundant the flies the longer a high level of activity continues, at dawn there is a second and less intense period of activity.
(5) Adult females do not seem to prefer any area of the human body for biting, except the head of African boys is apparently a preferred site.
(6) Feeding to repletion by females requires 1 minute 45 seconds to 12′ 40″ with an average time of 4′ 45″.

(Complete paper published in Journal of Medical Entomology, vol. 1, no. 3, 1964).

REVIEW OF OBSERVATIONS ON THE FEEDING, LONGEVITY AND FLIGHT RANGE OF SIMULIIDS AND CERATOPOGONIDS

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This review on Simuliidae will appear in more detail in volume 15, Experimental Parasitology, 1964, although the latter contains no reference to the work of Fallis and Smith on attraction to olfactory stimuli.

Feeding habits of the Ceratopogonidae were reviewed briefly by Downes (3). Several that feed on vertebrates transmit viruses, protozoa and helminths (5) although the amount of blood ingested at any one time may only be 0·05 cu. mm. (4). Some species prefer mammals, others birds and a few feed on amphibia (3, 13, 10, 1). Our work has shown some habitat as well as host specificity for several flies. For example *Culicoides downsi*, a vector of *Haemoproteus* to ducks, feeds extensively on ducks at the lake shore and to a lesser extent on birds in the forest canopy. *C. crepuscularis*, *C. sphagnumensis* and *C. stilobezzioides* are taken from birds in the latter habitat and usually 10 feet or more above ground. Until recently the only method of collecting females of this species in large numbers was from birds exposed in this habitat. These ornithophilic species feed after dark as well as at dusk indicating attraction to odour and/or heat. Several species are attracted to light traps and Kohler and Fox (8) found those painted chrome yellow were superior to those painted forest green. *C. impunctatus*, an annoying pest of man, shows peak activity a few hours after sunset and at sunrise, with less during dull days and calm, warm nights (6, 9).

Data on longevity are derived mostly from observations on females held in captivity following a blood meal. We kept *C. obsoletus*, *C. downsi*, *C. crepuscularis*, *C. sphagnumensis*, *C. stilobezzioides* for three weeks but natural survival is probably longer.

Flight ranges of about one mile have been observed for *C. impunctatus* (7, 9) and for *Leptoconops kerteszi* (11); *C. furens* moved 1·5 miles against the wind and 4 miles with it (2, 12).

The review indicates that knowledge of the feeding and related behaviour of species of Simuliidae and Ceratopogonidae is expanding although few data are available on the relative importance of carbohydrate and blood in the diet of blood-sucking species. Progress in understanding the attraction of various species to different stimuli was reported; the results suggest interesting possibilities for further research.

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STUDIES ON THE DISPERSAL OF *LEPTOCONOPS BEQUAERTI* KIEFFER DIPTERA: CERATOPOGONIDAE) BY MEANS OF WIND TRAPS

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Leptoconops bequaerti Kieffer. one of the three main pest midges found along the coast of Jamaica can cause considerable distress because of its painful and irritating bite. To overcome

the limitations of hand catching on human bait as a method of assessing population density, a wind trap has been developed which catches not only hungry females, but males and gorged or gravid females also. This suggested that it might be a useful tool for ecological studies.

The trap consists of a conical net of fine nylon bolting cloth having an opening of two square feet in area. This is suspended in a wire frame which is kept pointing into the wind by means of a vane. At the apex of the net, the insects are trapped in a container lined with a sticky band. The optimum catching position is 3ft. above ground for this species. Identical traps have the same catching ability and the trap is not attractive in itself, but catches through the action of the wind.

If two-hourly catches are compared with wind velocity, it transpires that both males and females are airborne in winds in excess of 20 mph. and that activity appears to be associated with wind velocity in the morning but not in the evening. Maximum densities are found between 12 noon and 16 hrs. 99% of the insects are taken below 10 ft. and only one (a hungry female) was taken at 38·5 ft. in 20 weeks of continuous trapping. There is a linear relationship between Log. density and Log. height.

By operating one trap continuously for 70 weeks the seasonal population variation has been studied. It has been found that density is proportional to the rainfall two weeks previously, and there is apparently a linear relationship between Log. rainfall and Log. density.

By placing 7 traps in a pattern on an artificial island near the coast, and by placing 5 more traps in a line downwind of the island at distances from 900 yds. to 5,000 yds. it has been possible to trace the main source of *L. bequaerti* to a particular part of the island, and also to plot the regression of density on distance from this source.

Although there was considerable variation in the numbers caught the general picture is clear. Regardless of the initial population near the source, the density was considerably reduced by 1,500 yds. At over 2,000 yds. it is doubtful whether the numbers are significantly greater than those caught by "control" traps upwind of the source. However, the fact that midges of both sexes, and especially gravid females, can be caught at over 5,000 yds. should not be overlooked if eradication is to be achieved. It is doubtful whether biting female *L. bequaerti* would be sufficiently numerous at distances in excess of one mile to cause a nuisance.

The foregoing account indicates some of the possibilities of such a trap used in connection with small biting insects, and one wonders whether it would be suitable for other genera, for example the Simuliidae, or for *Culicoides* in other parts of the World.

THE FEEDING BEHAVIOUR OF HAEMATOPHAGOUS DIPTERA IN RELATION TO THE TRANSMISSION OF TRYPANOSOMES AND VIRUSES

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The author, having transferred recently from the research field of the arboviruses to that of the trypanosomes, attempts to draw comparisons between the two fields which are useful for bringing the problems of trypanosomiasis epidemiology into perspective and in orientating future research.

Field studies on the arboviruses have in general been ecologically orientated, taking into account simultaneously all the various factors concerned, the wild animals, the arthropod vectors, and man. By contrast, work in the field of trypanosomiasis, because of the greater complexity of the problem in general, of the lack of the tools required to study certain aspects important for epidemiological understanding, and of the pressing health and economic importance of trypanosomiasis, has tended to concentrate on vector ecology with, as a main aim improvement in vector control as a "key" measure for the prevention of trypanosomiasis. Recent developments, however, particularly the introduction of effective therapeutic and prophylactic drugs and advances in experimental and immunological techniques which seem to offer better tools for epidemiological studies, have influenced a broadening of research approach in trypanosomiasis.

There are, however, many difficulties in the way of the application of the ecological approach in the field of trypanosomiasis as compared with that of the arboviruses. Serological

methods for the identification of pathogenic trypanosomes in wild animal hosts are not yet available as a multitude of trypanosome species, strains and antigenic types are under simultaneous transmission and serum antibodies are not clearly and categorically referable to pathogens of main interest. Practicable microscopy cannot recognize all the infected hosts. Thus the relative importance of different host species as potential sources of infection cannot be assessed as easily as it can be with the arboviruses. In the vector, only taxonomic groups of trypanosomes, not species, may be recognized. Although only a few *Glossina* species present themselves as likely vectors in any situation, *Glossina* are less easily susceptible of study on a quantitative basis than are mosquitoes; they may be important vectors at low population densities; they are more difficult to sample informatively.

Some biological aspects of trypanosomiasis are considered under the headings of the natural cycle of maintenance of the trypanosomes and of the routes of transference of organisms from the natural cycles into man and his animals. We know less of the patterns of behaviour of African antelopes in relation to *Glossina* than we do of the behaviour of African monkeys in relation to the mosquito vectors of yellow fever virus. The major contribution in the sphere of *Glossina*—wild animal relationships comes not from direct study but from the serological identification of blood meals. *Glossina* spp. show characteristic feeding patterns, usually attacking a wide range of animals but concentrating on a few. The mechanism of determination of these feeding patterns is obscure, but visual, olfactory and temperature stimuli, mechanisms relating *Glossina* to particular sections of the environment, and irritability of hosts seem likely to be important. Examples are cited of effects related to size and colour of host, to the attractiveness of skin constituents, to carbon dioxide concentration, and to the localisation of *Glossina* in certain sections of the environment. Attention is drawn to the differences in distribution of *Glossina* attack on the several parts of the body in different animal species and to the differences in irritability under attack between animal species. The selectivity of *Glossina* in the utilisation of hosts and the irritability of some hosts under attack point to the possibility that individual competition for food may be a factor in the limitation of *Glossina* populations, and may contribute to the evolution of different temporal biting patterns by different species. In general, it is important to base studies on a variety of methods of sampling and concurrent study of the biology of the mammal hosts would contribute to the orientation of entomological studies.

As regards the mechanisms of maintenance of pathogenic trypanosomes in wild animals, the host "spectrum" of the *Glossina* spp. may be taken as indicative of the degree to which each species acts as a vector link between individuals of the wild mammal population. Besides this, however, the chances of transmission depend on the number of bites occurring per unit time, the infectivity of the donor host to *Glossina*, the efficiency of the *Glossina* species as vectors and the receptivity of the recipient host. Infectivity of hosts to fly is difficult to assess as microscopically-recognisable parasitaemia is not a prerequisite for the infection of *Glossina* and wide differences may exist in the proportion of flies becoming infected by feeding on animals with apparently similar parasitaemias. Most quantitative work on trypanosomes has been related to numbers of organisms; in fact, infectivity is usually of more direct interest. Quantitative study of the infectivity of blood forms to fly would be advantageous, perhaps by methods similar to those developed recently for the measurement of their infectivity to other mammals. The xenodiagnostic use of standard laboratory-bred *Glossina* populations is perhaps another way of estimating infectivity of mammal hosts to fly. The detection of antibodies to trypanosomes in the blood meals of *Glossina* offers perhaps ultimately the prospect of adding significant knowledge of the antibody status of the animal fed upon, to that of its species. Immunology also, seems the approach most likely to provide ways of summing the infections occurring in host animals and of identifying particular pathogens in *Glossina* in the field. Until it is possible quickly to identify each of the pathogens of main interest in the field wherever they occur in the course of the cycles of transmission, it will not be possible to analyse epidemiological situations satisfactorily. It is in default of tools for this purpose that cattle trypanosomiasis has tended to be regarded as a whole, irrespective of the trypanosome species causing it. But clearly each trypanosome species can be expected to occupy its own individual ecological niche and so to differ in transmission pattern from other populations.

Assessment of the risk to which man and his cattle are exposed from trypanosomiasis should

begin from studies of their biology and behaviour and this basis should indicate how the *Glossina* population should be sampled. For instance, the *Glossina* sample taken by the fly-round may not be representative of the population infecting man. Recent work on the epidemiology of *T. rhodesiense* sleeping sickness in Busoga, Uganda, has very informatively been related to the biology of the human population; corresponding study of the biology of cattle in relation to their reception of trypanosome infections would be advantageous.

In conclusion, the difficulties in the way of the development of epidemiological studies on trypanosomes comparable in informativeness to those on the arboviruses are primarily in the lack of tools for deriving quantitative information from the field. For future progress there is need of a stable team comprising all the disciplines needed for comprehensive ecological studies, concentrating on a few selected areas, and in close contact with basic research laboratories likely to be able to assist in contributing the additional tools of investigation of which we are still in need.

THE INFLUENCE OF IRREGULARITIES IN THE BUSH PERIMETER OF THE CLEARED AGRICULTURAL BELT AROUND A GAMBIAN VILLAGE ON THE FLIGHT RANGE AND DIRECTION OF APPROACH OF A POPULATION OF *ANOPHELES GAMBIAE MELAS*

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Daily observations for over one year were made on populations of *A. gambiae melas* travelling over 1-2 miles between their brackish breeding grounds and a village in quest of food.

This journey, necessary for the completion of each gonotrophic cycle, forced the mosquito coming from the mangrove swamps to cross orchard bush and open cultivated land before reaching the village.

Three concentric rings of traps were used for this work. Nine were placed along the swamp littoral and 8 formed a circle ($\frac{1}{2}$ mile radius) around the village on the outer fringe of the peri-urban cultivated land. A further 20 traps around the village and six within the village formed the innermost ring.

The traps of the outer rings were baited with goats while those around and inside the village were baited with cattle. Goats were an efficient bait as long as they were not in competition with other animals, while cattle were the favoured host of *A. gambiae melas*.

From this study the following conclusions have been developed.

(1) High density populations generated at any given point on the swamp perimeter did not approach the town in a straight line.

(2) The bulk of the mosquito population entering the town crossed the peri-urban cultivated area in 5 well defined and narrow avenues, forming, at peak mosquito season, high density mosquito streams about 20-60 ft. wide flying between five feet and ground level.

(3) Mosquito traffic on the five approaches varied with season.

(4) Five feet high stake or corn wattle fences around village compounds were sufficient to divert or channel the stream of mosquitoes.

(5) Wind direction did not determine the direction or pattern of mosquito approach to the village although it did determine the side on which mosquitoes made the final approach to the trap or habitation. The coincidence of long periods of calm nights with other favourable meteorological conditions increased the longevity of the mosquito population.

(6) Mosquitoes approached the town by following the interface between bush and cleared land. Approach streams arose and left the bush perimeter from bush promontories projecting into the cleared area, often following lines of planted trees or wide paths. Funnel clearings in the bush belt also produced high densities at their narrow (village) ends.

(7) Under these conditions the placement of a trap at random to estimate presence and density of mosquitoes could be most misleading.

(8) Two traps even when located side by side 30 ft. apart are not comparable; when in tandem and oriented to the mosquito stream the first trap or house received most of the inflying population.

(9) The pattern of approach remained constant as long as the configuration of the bush perimeter was not changed.

(10) With this knowledge would it be possible to divert and trap the inflying mosquito streams and thus cheaply eliminate the bulk of the population?

STUDY OF THE FEEDING HABITS OF MALE *ANOPHELES SERGENTI* THEO. AT SIWA OASIS USING RADIOPHOSPHORUS

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Little has been published on the feeding habits of male mosquitoes, and the subject has not previously been investigated in respect of the important oasis malaria vector, *Anopheles sergenti*. The present WHO-sponsored study was designed to investigate the suitability of the various plants of an ecologically isolated habitat as food for male *A. sergenti* Theo., and the natural feeding habits of these insects. The project was undertaken at Siwa Oasis, from 19th May to 28th June 1963.

Male *A. sergenti* needed for experimental purposes were reared in a field laboratory from larvae brought in from the field. Drainage canals from the springs and seepages, proved to be the most favoured larval habitats. The different plants present in and around the larval habitats of *A. sergenti* were collected and brought to the laboratory for experimental purposes. In the laboratory, the cut end of a stem from each plant (carrying leaves, and flowers where present) was wrapped in a piece of cotton and immersed in 30 ml of 20 microcuries per ml of sodium radiophosphate (Na $H_2P^{32}O_4$) in distilled water inside a 50-ml wide-mouth bottle. The opening of the bottle was then covered with cheese cloth to prevent the mosquitoes from coming into direct contact with the radio-active solution. Every plant exposed to radiophosphate was set aside for 24 hours before being placed inside an experimental cage having the top and sides of metal screening, and a sliding glass front. Fifteen *A. sergenti* males were introduced into the experimental cage through a 5-cm opening in the centre of the glass front, which was then closed with a cork. The males were left for 48 hours with the radio-active plant. After that exposure time, all the mosquitoes inside the cage were taken out, killed, if still alive, by chloroform vapour, and washed in three changes of distilled water. After being dried between two pieces of filter-paper, each was transferred to the centre of a copper planchet and was covered with a piece of sellotape. The mosquitoes on the planchets were now assayed for their radioactivity.

The results of these experiments showed that out of forty different species of plants both wild and cultivated, belonging to 24 families and representing almost every species encountered in the oasis, only three proved suitable as food for *A. sergenti* males. These plants, in descending order of their importance in this respect were: *Salicornia fruticosa* (L.) L., *Alhagi maurorum* Medic. and *Juncus arabicus* (Asch. et Buch.) Adams. These three species grow wild in different parts of Siwa, in and around the breeding sites of *A. sergenti.* Males of this anopheline were subsequently collected from them in the field in much greater numbers than from other plants. They comprise a relatively small proportion of the local flora, and should further studies prove the males of this anopheline unable to adjust to alternative food sources, it is submitted that their selective control could be of practical vector control significance—for example, in lowering the normal ratio of *A. sergenti* males to females immediately prior to the mass release of males sterilized by means of chemosterilants or radioi-sotopes.

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TAXONOMY AND DISTRIBUTION OF ARTHROPODS OF MEDICAL IMPORTANCE

THE SPECIES IN MEDICAL ENTOMOLOGY, WITH EXAMPLES FROM MOSQUITOES

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SUMMARY. Within a local area most species are distinct, but a few are usually complex and difficult. With examples from mosquitoes it is shown how the biological species concept usually permits an understanding of complex species.

The medical entomologist who applies the concept should find the terms *species group*, *species*, *subspecies*, and *variety* sufficient for classifying the forms he encounters. For discussing their biology he will need additional terms, without nomenclatural status, such as polymorph, ecotype and insecticide resistant strain.

DEFINITIONS. *Species* are groups of actually or potentially interbreeding populations reproductively isolated, and usually morphologically distinguishable, from other such groups. —Mayr, 1942 (modified).

A *subspecies* is an aggregate of local populations of a species, inhabiting a geographic subdivision of the range of the species, and differing taxonomically from other populations of the species.—Mayr, 1963.

LOCAL AREAS. Field workers are concerned with their own local area, so this will be our starting point. In any local area most species are distinct, but some are troublesome to identify, usually because they seem to occur in more than one form. Some do so within the local area (*sympatric complex*) others have one form in the local area but different forms in adjacent areas (*allopatric complex*).

SYMPATRIC COMPLEX. Among mosquitoes there are two main kinds of sympatric complex; the commonest and most important is the kind which proves to be a group of sibling species; the second kind is the polymorphic single species.

Sibling species.—These are good species, fully reproductively isolated and ecologically distinct, but with minimal morphological differences. The classic example is the *Anopheles maculipennis* group in Europe (1). Many others are now known, and probably the *Anopheles gambiae* complex in Africa is another (2).

The recognition of sibling species in a local area depends, as for other species, on the demonstration or inference that sympatric forms which can be distinguished in some way, are also reproductively isolated. With ordinary species reproductive isolation can usually be assumed from the morphological differences, but with sibling species these differences are so small that more direct evidence of reproductive isolation is desirable. With mosquitoes this can often be obtained by examining the progeny of wild females to see if all are of the same form as their mothers.

Although sibling species may be troublesome to identify there is no doubt of their importance. Until the *Anopheles maculipennis* complex was unravelled the epidemiology of malaria in Europe was in confusion. About half the Malayan anophelines belong to groups of sibling species, including several of the vectors of malaria and filariasis (3). Even so it is not always necessary to identify a specimen further than its species group, labelling it, for example, as *Anopheles hyrcanus* group.

Polymorphic and variable species.—These are species which occur in more than one form at one place, but unlike sibling species, the forms are found to interbreed and are evidently variants of one species. Such forms need not be named unless very distinct when they are best called varieties.

Aedes aegypti (4, 5) shows a range of colour from black to pale yellow. Black forms are commoner outdoors and bite other hosts as well as man; pale forms (var. *queenslandensis*) are domestic and man-biting; but crosses between the two are fertile and all gradations can be found in nature.

Culex pipiens (6) exists in a number of forms that differ more in biology than morphology.

Variety *molestus* occurs as scattered populations within the range of *pipiens* from which it differs in northern Europe by being autogenous (laying eggs without a blood meal), stenogamous (mating in small spaces), man-biting, non-hibernating, a cryptic breeder in cellars, etc., and usually being paler in colour. The puzzle about *molestus* is that some geographically separated populations are intersterile (7), but since crosses between *molestus* and *pipiens* are often fertile, and intermediate populations occur in nature or can be derived by selection from *pipiens*, it seems that *molestus* is not a distinct species. More probably *molestus* is the name for separately arising populations of *pipiens* with high gene frequencies for such adaptive characters as autogeny and stenogamy (8), in other words an ecotype of *pipiens*.

Insecticide resistant strains belong here, for the susceptible and resistant genotypes of a species are sympatric but interfertile.

ALLOPATRIC COMPLEX. Many species have different forms in different parts of their range. If these geographically separated forms are distinct enough we call them subspecies; these will interbreed if they meet and it follows that two subspecies cannot be sympatric and it is wrong to call sympatric forms subspecies.

It is often difficult to decide whether allopatric forms are subspecies or full species, since we cannot see, as we can with sympatric forms, whether interbreeding can occur or not. This difficulty, plus the inconvenience of trinomials, has led some systematists to call all allopatric forms species (9), but this is simply a return to the morphological species concept.

With mosquitoes, where little is yet known about geographic variation and many sibling species remain to be detected and convenience is important, it seems best to be conservative in naming subspecies. Even when subspecific names have been given, it may not be necessary to use them within a local area where each species will usually be represented by only one of its subspecies.

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PHYLOGENY OF *HAEMAPHYSALIS* TICKS*

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The genus *Haemaphysalis*, at this term in our knowledge of ticks, appears to be the most suitable indicator of phylogenetic progression and speciation in the Ixodoidea. *Haemaphysalis* contains approximately 100 species plus 15 subspecies and a greater proportion of known associations of larvae, nymphs, males, and females than any other ixodid genus. Structural and biological features characteristic of each developmental stage and sex of the 115 species and subspecies thus provide approximately 460 units for comparative study within the genus.

Eight structurally primitive species in four subgenera link *Haemaphysalis* and other ixodid genera and differ distinctly from over 100 other haemaphysalid species. The most basic criterion among these eight species is the presence, in all stages or in larvae and nymphs only, of a laterally projecting basis capituli. Next most basic, their palpi are elongate or compact

* The opinions and assertions contained herein are the private ones of the author and are not to be construed as official or reflecting the views of the Navy Department or the naval service at large.

but never basolaterally salient. Spur development is, with certain few exceptions, exceedingly slight. In all other haemaphysalid species, the basis capituli is rectangular with posterior cornua rather than lateral projections. The phylogenetic trend throughout the genus is towards widely basosalient palpi and considerable adaptation of spurs and angles of body appendages to assist the small tick in reaching the host integument through a maze of stiff hairs or feathers.

The type and degree of palpal and spur development is closely correlative with the type of host each haemaphysalid species prefers. Immature stages of seven of the eight structurally primitive species feed on lizards while those of almost no others do so. For this and other reasons, it is suggested that ticks may have been associated with reptiles in the late Paleozoic or early Mesozoic Era, that the morphologic frame of the eight "primitive" species is rather like that of their reptile-parasitizing progenitors, and that obsolescence or modification of this pattern in other haemaphysalid species represents specialized adaptation to bird and mammal hosts.

When birds appeared on the earth, haemaphysalids adapted to and flourished on them. The basis capituli became rectangular, and persisted in this form throughout history, and the palpi become basolaterally salient. Spurs, however, continued to be slight or very moderate in size and variety. Bird-parasitising species, characterised by considerable uniformity, fall into two groups, those that feed only on birds and those that feed both on birds and on certain small to medium size mammals.

With the coming of mammals, the comparatively latent phylogenetic trend to spur development awakened; a variety of adaptive spurs was added to haemaphysalid capitular and leg appendages. Palpal basosalience was generally enhanced but in certain species a reversal of this trend, in the form of non-salient palpi, occurred in the nymphal stage or in both adult sexes or in either the male or female sex. Somewhat over half of the contemporary haemaphysalid species feed only on mammals and have a marked preference for certain host species, genera, or families.

Warm, humid forests of tropical Asia and adjacent islands contain approximately 50 species, none of which is structurally primitive. In this area, two or three species are often found on the same host. Haemaphysalids probably originated here but primitive forms became extinct possibly owing to severe competition from more recent forms. Temperate Asia, Europe, and the Near East harbor approximately 20 species, seven of which are structurally primitive. Adults of these seven species often feed during colder months of the year when chances for desiccation are least. Notably, adults of these seven species are among the very few haemaphysalids that have adapted to domestic herbivorous mammals, a host pattern that may have contributed to the survival of their old morphologic form. The presence of large coxal spurs in males of two of these seven suggests that these two species are comparatively recent members of this ancient assemblage.

Islands of the Madagascar group have 9 species, one of which is structurally primitive and parasitizes one of the most primitive of placental mammals, the insectivorous tenrec. In Australia and New Guinea, with nine species, tropical Africa, with ten species, and the Americas, with three species, no structurally primitive forms are found. Notably, Australian species that parasitize marsupials, the most primitive of mammals, are characterized by very slight spur development and uniformity of the widely basosalient palpi.

Thus, in this genus, a combination of structural and biological features furnish clues to phylogeny and speciation. A three-volume monographic revision of this genus is presently in preparation.

THE RELATIONSHIPS OF NEARCTIC AND PALAEARCTIC SIMULIIDAE (DIPTERA)

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Opinion is divided as to the number of full genera that should be recognized in the Simuliidae. Following F. W. Edwards and other workers in Nematocera, and in accordance with the recent plea by R. W. Crosskey to restrict the number of genera, I have accepted for the Holarctic Region only 7 genera, 3 of which are divided into 21 subgenera. Of the 25 genera and subgenera, 7 are strictly Old World, 7 strictly New World, and 11 are found in both regions. There appear to be at least 12, and possibly 14, species that are Holarctic. The 774 published names of the species group, representing about 54% of those for the world, are very unevenly divided between the Old World and the New World. There are 435 species, 94 infraspecies, and 75 synonyms in the Palaearctic Region, and 102 species, 1 infraspecies, and 55 synonyms in the Nearctic Region. Certainly many species are still undescribed in North America, but it is possible that more have been named from Eurasia than actually occur there. Proportionately, many more infraspecies are recognized in Europe and many more synonyms in America.

Two taxa require some explanation because their type species have not been fully described. The first is *Cnephia* Enderlein, with type *Simulium pecuarum* Riley. The type species falls into the *Cnephia lapponica* group, possessing some characters close to those of *lapponica* (Enderlein), others more like those of *intermedia* Rubzov. The second is *Byssodon* Enderlein, with type *Simulium forbesi* Malloch, a synonym of *S. meridionale* Riley. This species is extremely close to, and possibly a synonym of *S. maculatum* Meigen, the type of the subsequent *Titanopteryx* Enderlein. *Byssodon* as interpreted by Rubzov, includes the possibly Holarctic *B. transiens* Rubzov which is related to the American species *S. slossonae* Dyar and Shannon and *S. rugglesi* Nicholson and Mickel. These three species form an atypical group, but I would retain them in *Byssodon* Enderlein because the females possess deeply cleft claws and there are no setae on the basal section of vein R.

Of 14 species that have rather currently been considered as Holarctic, *Prosimulium hirtipes* (Fries) is probably not found in America, and the record for *Cnephia mutata* (Malloch) is probably erroneous for Japan. *Prosimulium alpestre* Dorogostajskij, Rubzov and Vlasenko, *P. ursinum* (Edwards), *Simulium baffinense* Twinn, *S. bicorne* Dorogostajskij, Rubzov and Vlasenko, *S. malyshevi* Dorogostajskij, Rubzov and Vlasenko, and *S. rubtzovi* Smart are all boreal and probably circumpolar. *Simulium aureum* (Fries), *S. latipes* (Meigen), and *S. tuberosum* (Lundström) are species complexes and much more study is needed to determine whether any of the component sibling species are Holarctic. *Simulium venustum* Say and *S. verecundum* Stone and Jamnback are apparently found in typical form on both sides of the Atlantic. Finally, because *Simulium nölleri* Friederichs is considered to be a synonym of *S. argyreatum* Meigen by Rubzov and because I consider *S. decorum* Walker to be the same as *nölleri*, I would adopt the name *argyreatum* for the species now known as *decorum* in America.

INSTAR RECOGNITION IN *AEDES* LARVAE (DIPTERA: CULICIDAE)

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Although most existing keys for the identification of *Aedes* mosquito larvae are based upon characters of the mature (fourth instar) larva, little has been published on recognition characters for the various instars, except for the first, which is readily identified by the pointed egg-breaker and the bi-colored siphon. In the present study, twenty-six species of *Aedes* from eastern North America were examined in an effort to discover characters useful in separating instars.

The fourth instar, in those species in which the anal segment is not completely encircled

by the saddle (a fourth instar character), can be recognized most reliably by the position of the saddle hair and the shape of the saddle. The hair (except in one North American species, *A. atropalpus*, is inserted on the saddle at a point nearer the posterior than the ventral margin. (In those species with notched saddles, measurements are made from the lowest point of the saddle.) The saddle itself is quadrangular, with posterior and anterior margins usually nearly vertical and parallel, the lower corners scarcely rounded.

In earlier instars, the saddle hair position may vary, even within instars of a given species. It may be inserted on the membrane below the saddle. This is typically a second-instar position, occurring in at least some individuals of all but three of the twenty species studied in this instar (and probably in these if more specimens were to be examined), and ranging from about two per cent of the specimens seen of *abserratus* to nearly ninety per cent of *fitchii*, with an average of forty-five per cent. In five species, including *atropalpus* and *vexans*, this position is constant in both second and third instars, and is also seen in from five to seventy per cent of third instar individuals of five additional species. In the third instar the hair is more frequently located on the saddle, on or slightly above its ventral margin. Sixteen of the species are constant in this position in the third instar, although fifteen of the twenty species examined in the second instar had at least some individuals with hairs in these positions. In the first three instars, the saddle itself is broadly rounded laterally, without distinct lower corners. In those few cases in which the saddle hair is located nearly equidistant from ventral and posterior margins, the shape of the saddle itself will almost invariably separate third from fourth instar.

Other characters examined are of value within a given species, but no single criterion was found to be reliable in separating all second from all third instar larvae. The width of the head capsule; the ratio of adult to larval eye; the ratios between head and collar, head and labial plate, labial plate and foramen; the shape of the siphonal apodeme; and the length-width ratio of the siphonal atrium or felt-chamber all are useful and often reliable characters to differentiate the instars within a given species but show too much variation between species to serve as instar indicators of unknown larvae.

CERTAIN RESULTS OF THE STUDY OF BITING MIDGES (DIPTERA: HELEIDAE) IN THE U.S.S.R.

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The present report contains certain results of work carried out by the author and by others including Montchadsky, Dzhafarov, Glukhova, Remm, Molev, Shakirzjanova, Krivosheina, Bujanova, Mirzaeva, Muradov.

Bloodsucking midges, i.e. insects belonging to the genera *Culicoides*, *Leptoconops* and *Lasiohelea* are widely distributed over the territory of the USSR. *Culicoides* species occur in all topographical zones reaching to the northern border of the forest zone and penetrating in some localities into tundra (*C. fascipennis* Staeg., *C. pulicaris* L.). *Leptoconops* midges in the European part of the USSR are distributed approximately to the latitude of Moscow (*L. borealis* Gutz.). Biting midges of the genus *Culicoides* are the most numerous in forests of Siberia and of the Far East, *Leptoconops* midges—in the region of arid steppes of the Caucasus and Central Asia.

The list of biting midges registered over the territory of the USSR includes 101 species of *Culicoides*, 11 species of *Leptoconops* and 3 species of *Lasiohelea*, in all 115 species, many being new. The number of species of bloodsucking Heleidae sharply increases in the direction from the North to the South. So in the Tomsk region (Western Siberia) 21 species were recorded (Mirzaeva, 1964), in Transcaucasia—75 species (Dzhafarov, 1964), in Central Asia—57 species (the author's data), among them the large group (21 species) of *Culicoides* with unspotted wings.

The number of species of important biting midges is relatively not high. In the forest zone *Culicoides pulicaris* L., *C. grisescens* Edw. and species of the groups *obsoletus* and *fascipennis* are

prevalent, in steppe—*C. riethi* Kieff. and *C. pulicaris* L., in arid steppes and semideserts—*C. puncticollis* Beck., *C. saevus* Kieff., *C. desertorum* Gutz. as well as *Leptoconops* spp. (in river valleys).

Mountain *Culicoides* species form a distinct ecological group, some of them being recorded only in the mountain regions: *C. chaetophthalmus* Amos. and *C. setosus* Gutz. (Sikhote-Alin, the Caucasus, the Carpathians), *C. latifrontis* Shak. (the Altai, Alatau, the Ural, the Caucasus, the Carpathians), *C. montanus* Shak. (Alatau, Kopet-Dagh). In humid mountain forests up to heights of 1500-2000 m the abundance of biting midges can be high (Sikhote-Alin, some areas of the Caucasus and the Carpathians).

It is remarkable that biting midges are rather numerous in some arid regions of Central Asia even in places where natural waters are absent. In such areas the development of *Culicoides* is closely connected with irrigating systems and wells. In arid southern regions the curve of *Culicoides* seasonal activity has two peaks and a great reduction at the hottest time.

It has been proved that *Culicoides* may have repeated gonotrophic cycles; females of *C. grisescens* Edw. were found to have two, three or four enlargements of ovarial tubes (Glukhova, 1958).

The abundance of midges attacking men and domestic animals sometimes does not correspond to the total density of biting midges in nature. Such species as *Culicoides odibilis* Aust., *C. circumscriptus* Kieff., *C. saevus* Kieff. very seldom attack human beings even if the midges are very numerous (this has been ascertained by catching at light and by rearing from pupae). Many species apparently feed on wild mammals and birds.

THE DISTRIBUTION OF FLEAS IN THE MIDDLE EAST

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While North Africa exhibits numerous examples of its faunal affinities with the Ethiopian faunal region, its relation to the Palaearctic is undeniable. With respect to the Siphonaptera of North Africa there are a few examples of southern European species which have crossed the barrier of the Mediterranean Sea. The majority of the species which occur there, discounting the cosmopolitan forms, are either unique to North Africa or are descended from typically Asian genera and subgenera.

Members of the subgenus *Gerbillophilus* of the genus *Nosopsyllus* provide one example of a group of probable Asian origin which occur in North Africa. *Nosopsyllus* (*G.*) *maurus* and three of the four subspecies of *N.* (*G.*) *henleyi* occur exclusively west of the Suez canal. Eight additional species and subspecies range through southwest Asia while the remaining twelve forms are Russian in their distribution.

It is particularly interesting that the obvious land connection between southwest Asia and North Africa, the Sinai Peninsula, is the area whence two new subgenera have been taken in the past ten years. In addition it supports species belonging both to *Gerbillophilus* and *Nosopsyllus s.str.* as well. Additional field work in this region is bound to be rewarding.

A second example is found in the nominal subgenus of the hystrichopsyllid genus *Rhadinopsylla*. Of the six species presently recognized, four are Russian in their distribution. The fifth, *Rh. masculana*, occurs in North Africa. The sixth form, *Rh. syriaca*, while most nearly related to the Russian *Rh. cedestis*, connects the range of the North African form with those from Central Asia. All species are typically ectoparasites of gerbilline rodents and their collective range roughly matches the distribution of their hosts.

A third example involves the monogeneric family Coptopsyllidae. Sixteen species and subspecies are presently recognized, twelve of which occur exclusively in Russia and the northern tier of Middle Eastern countries. Two more are exclusively North African and the remaining two are Middle Eastern. Both of these latter species appear to be closely related to Russian forms. The African forms, on the other hand, have apparently been isolated long enough to have lost at least their obvious affinities; *C. africana* less so than *C. wassiliewi*.

One of the most interesting examples of the faunistic link between Asia and North Africa

involves the members of the amphipsyllid genus *Caenopsylla*. The two most highly modified species *C. mira* and *C. assimulata* are known only from a restricted area in Algeria and Tunisia. While very few specimens have been taken, they were both described over half a century ago. In 1958 a third species was described from Turkmenia and since has been taken from Iran, Lebanon, northern Saudi Arabia and northern Egypt near the Libyan border. This is a far less modified form and probably resembles the prototype of the genus.

As one progresses from north to south around the Eastern Mediterranean, the number of European species of fleas decreases noticeably. The habitat similarities between Central Asia, the Middle East and North Africa apparently permit certain species groups to occupy the entire area although individual species may only occur in a restricted portion of the territory.

THE NEOTROPICAL MITE GENUS *GIGANTOLAELAPS* FONSECA (ACARINA; MESOSTIGMATA: LAELAPTIDAE)

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As their name implies, mites of the genus *Gigantolaelaps* are exceptionally large, ranging from 1270 to 2070 micra in length. They have plump bodies thickly clothed with coarse setae, a short, posteriorly rounded genitoventral plate bearing one pair of setae, no post stigmal extension of the peritrematalia, and a triangular tectum. Males have a fully formed holoventral plate widely expanded behind coxae IV—typical of laelaptines in the strict sense.

These mites were reported to the world for the first time 60 years ago as *Laelaps*. In 1904 Berlese (Redia I: 259) described a *Laelaps maximus* from Uruguay and A. C. Oudemans described *Laelaps versteegei* from Surinam (Notes, Leyden Museum 24: 223) and *Laelaps wolfssohni* from Chile (Rev. Chilena Hist. Nat., 14: 147). Subsequently, in 1935, Flavio da Fonseca described several forms from Brazil under *Macrolaelaps* Ewing.

By 1939 Fonseca had found several more forms and he became convinced they represented a genus new to science. He proposed the very appropriate name *Gigantolaelaps* for them and chose as genotype a new species, *G. vitzthumi* Fonseca, 1939 (Mem. Instituto Butantan, 12: 7).

It is truly a neotropical genus, being found only in the new world between the latitudes 35°N. and 35°S., from Bull's Island, North Carolina (U.S.A.) to Montevideo, Uruguay. They have been reported from 3 species of marsupials, two species of carnivores, 6 genera and 12 species of non-cricetine rodents, and 15 genera and 36 species of cricetine rodents. They are most frequently found on cricetines of the genus *Oryzomys*—26 records from 12 species of *Oryzomys* have been reported.

The genus is a memorial to the late Dr. Flavio da Fonseca;—of the 17 species names proposed to date, 12 are by Fonseca. Two are by Oudemans and one each by Berlese, H. E. Ewing, and Harvey B. Morlan. Furman and Tipton (Mem. Soc. Ciencias Nat. La Salle, 21: 166, 1961) give new host and locality records from Venezuela for 5 species and also suggest that Ewing's species, *peruvianus*, is a synomym of *wolfssohni* (Ouds.).

New host and locality records here recorded for the first time are: *G. goyanensis* Fons., 75 ♀♀, ex. (rats) at Cumaca, Trinidad, June 1-21, 1954, by T. H. G. Aitken; *G. inca* Fonseca, 20+ ♀♀ ex. *Reithrodontomys* sp. at Omiltemi, Guerrero, (Mexico), Nov. 1, 1962 by A. Barrera; *G. oudemansi*, Fons., 3 ♀♀ ex. *Oryzomys* sp. at Belem, Para (Brasil), July 14, 1960 by Ottis Causey; *G. oudemansi*, 3 ♀♀ Fonseca ex "rats" at Cumaca and St. Pats, Trinidad, June 13, 1954 by T. H. G. Aitkens; *G. vitzthumi* Fonseca, about 25 ♀♀, several ♂♂ ex. *Oryzomys caliginosus* at Turrialba, Costa Rica, July 9, 1963 by Dale Birkenholz.

VECTOR-PATHOGEN RELATIONS OF BLOOD-SUCKING ARTHROPODS

DOUBLE INFECTION OF MOSQUITOES WITH A VIRUS AND A MALARIAL PARASITE

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In 1960, human malaria and malaria infections in vector anophelines (*Anopheles funestus* and *An. gambiae*) in Masaka district, Uganda, were unusually low. It was suggested that, besides other explanations, concurrent infections of the vectors with the arbovirus of the new disease O'nyong-nyong fever (ONN), which these mosquitoes were also transmitting that year to the African population, may have suppressed the developmental cycle of the malaria parasites in the mosquitoes (2).

A laboratory study of this proposition was made in London, using *Aedes aegypti* infected with Semliki Forest Virus (SFV) and *Plasmodium gallinaceum* from their respective vertebrate hosts, infant mice and fowls. Both pathogens infected the mosquitoes well, viz. means of 89% infection rate for SFV and 88% infection rate for fowl malaria from several experiments, justifying comparison of effects in *Aedes* harbouring both the virus and the malaria parasite. In general, the malaria parasite and its transmission were not usually affected by the presence of the virus in the vector, although malariometric indices were sometimes a little lower in doubly-infected *Aedes* than in controls (malaria infection only) and consistently so in mean oocyst counts per gut. Nor, generally, were the mosquitoes adversely affected themselves by the virus infection only, the malaria infection alone, or both infections combined. In one experiment, however, the doubly-infected *Aedes* died in large numbers (60% mortality) within 48 hours of taking a malarious meal 8 days after a previous SFV-infecting meal. Moreover, the survivors of this mortality were less heavily infected with malaria than the control malarious *Aedes*. The main comparative data were:

	Oocyst rate	*Mean Oocysts per gut*	*Transmission rate by bite*	*Total Malaria rate*
Control	75%	21	100%	83%
SFV + Malaria	46%	3	33%	42%

The total malaria rate was significantly different at $P < 0{\cdot}02$.

Thus, the kill of mosquitoes in this experiment was selectively in favour of survival of virus-infected mosquitoes negative for malaria or lightly infected with malaria. This mechanism was coupled with suppression in the individual mosquitoes of the intensity of their malaria infections. Either, or both, mechanisms together, may have operated with the anophelines in their transmission of ONN virus and human malaria in Africa. It is possible that, since human malaria infections in anophelines are much lighter than in this *Aedes* model, suppression of individual malaria infections in, rather than selective kill of, doubly-infected anophelines may have been more important. It is puzzling why, in the *Aedes* model, the marked effect was obtained only in 1 of 7 experiments. There are reasons, discussed fully in the main paper by Bertram, Varma and Baker (in the press) for suggesting that in this experiment the *Aedes* were less sturdy than in the other comparisons so that they were less able to withstand their double infections with virus and malaria. Thus, a physiological stress or deficiency in the vectors was necessary to elicit a reaction between the virus and the malaria sufficient to suppress notably the latter in its development and, indeed, to kill the more malarious mosquitoes. Zulueta *et al.* (3) note that anopheline densities were unusually high in Uganda in 1960; the general vitality of individual mosquitoes could be lower in high density populations and the stresses of life greater and render them less tolerant than normal populations of double infections. Under such circumstances, larval nutrition might, in particular, be sub-optimal and result in adults of low vigour and tolerance to infection; in the *Aedes* model, this larval factor could have been at play in the single experiment in which double infection caused high adult mortalities and lowered malaria infection in the vector.

It is of interest that the notable *Aedes* mortality and the marked, or more usually the slight, reduction of malarious infections occurred about the time when the mosquito gut cells, already subject for 8 days to SFV infection and replication, were being invaded by ookinetes of the recently-ingested malarious blood meal. Other experiments in which the SFV-infecting meal followed after oocyst formation was 3-4 days advanced from a preceding malarious meal, were particularly lacking in demonstrable interference by the virus with the transmission of the malaria parasite, nor was the survival of the vector notably affected.

In brief, malaria transmission by a mosquito can be suppressed severely by concurrent infection of the vector with an arbovirus, and the vector may itself be killed by the interaction, but this effect is by no means inevitable. It may become evident only if the vector is under stress or physiologically deficient; the critical factor(s) initiating sub-optimal tolerance of double infections may be larval nutrition, although direct stresses on doubly-infected adults may also be important.

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STUDIES OF CULICIDAE (DIPTERA) AND CONSIDERATION OF THEIR ROLE AS POTENTIAL VECTORS OF ARBOVIRUSES IN AUSTRIA

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Serological investigations have shown the presence of mosquito-borne viruses in Austria (3 and unpublished). Tahyna virus seems mainly to occur in meadows along rivers and Kunz has detected hemagglutination inhibiting antibodies for it in the sera of a high percentage of the population of Klosterneuburg (20 km. W. of Vienna). In 1963, a light trap was used for mosquitoes for virus isolations, from May 15 to September 15 on 54 nights and a total of about 6,000 female and 3,000 male *Aedes* was captured, as follows: *Aedes flavescens* Müll., *cantans* Meig., *annulipes* Meig., *excrucians* Walk., *punctor* Kirby, *sticticus* Meig., *vexans* Meig., and *cinereus* Meig. In addition 1-10 specimens per night were captured of other culicids, but, for clarity, these have been omitted from the graphs together with the male *Aedes*.

Ae. vexans, which is believed to be the main vector of Tahyna virus (1, 2) represented about 80% of all culicids. Continuation of these investigations showed:—

1. Correlation between fluctuation of the Danube water level and population dynamics of Culicidae (fig. 1);
2. Correlation between major meteorological factors and flight activity to artificial light (fig. 2).

The second of these shows how an optimal value for one meteorological factor cannot be stressed without taking other factors into consideration, as all operating together affect flight activity. Nevertheless, threshold values could be established for temperature +10°C, for RH 50% resp. 100%, for wind velocity 6 m/sec. Light rain hardly affects flight activity, but heavy rain causes flight to cease altogether. Stable atmospheric pressure shows a slight negative influence, while rapid changes are stimulating.

These results have shown that population densities have maxima of only short duration and that flight activity to artificial light is strongly influenced by meteorological factors, so that light traps must be considered unsuitable for collecting mosquitoes for virus isolations.

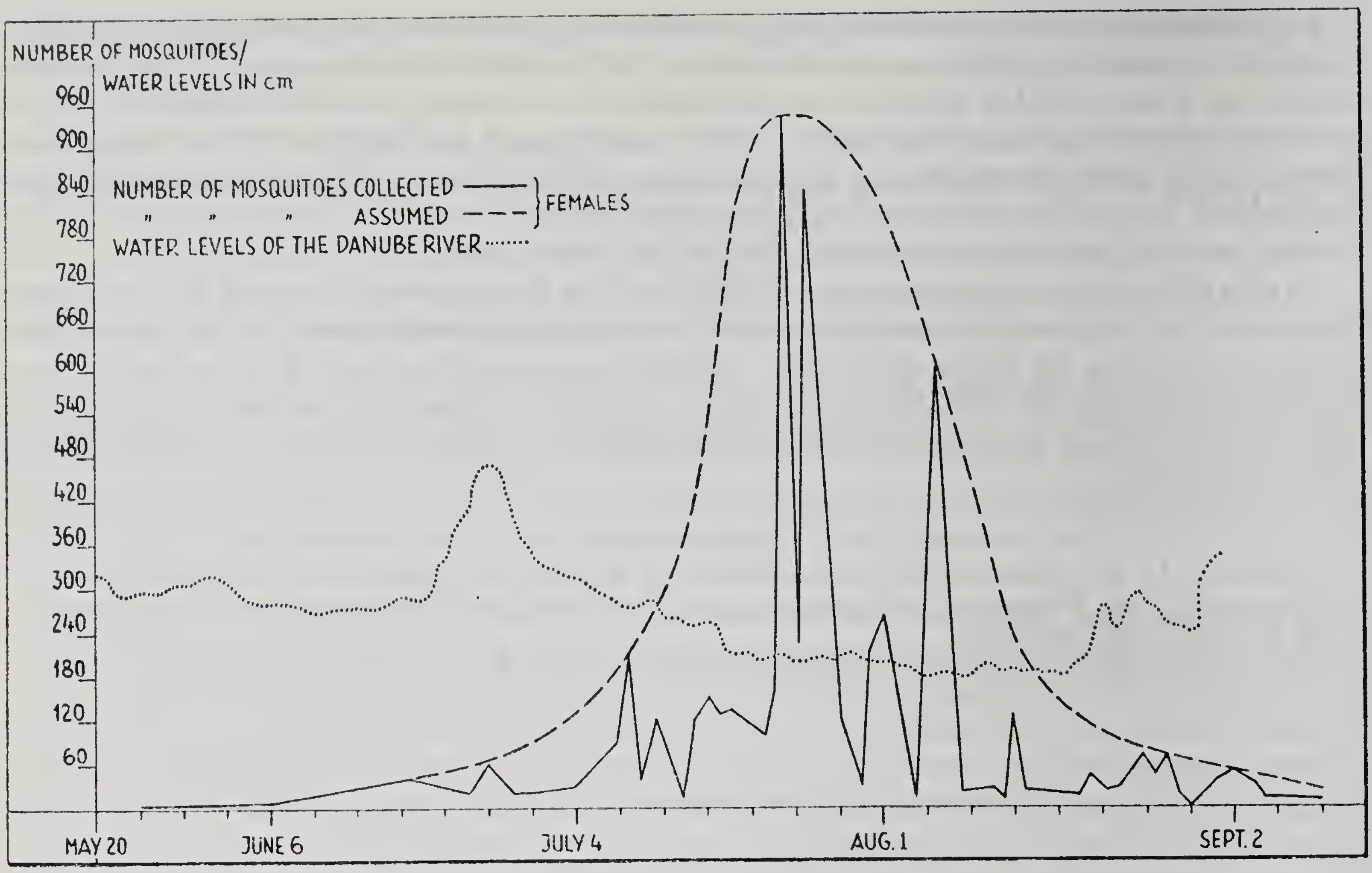

Fig. 1. Water levels of the Danube and seasonal fluctuations of mosquitoes near Klosterneuburg in 1963. (Annual average water level—257 cm.).

However they are an excellent method for studies of the population dynamics in natural foci of mosquito-borne viruses.

As can be seen from Fig. 1 the area investigated was nearly free from Culicidae up to the beginning of June, when only low populations of *Aedes cantans*, *flavescens*, *annulipes*, *excrucians*, *punctor* and *cinereus* were present. *Ae. vexans* did not appear before the middle of June. It is therefore apparent that the viruses cannot show in these habitats in spring as the population densities of the potential vectors are then much too low. As regards Central European mosquito-borne viruses, there are probably very complex cycles. All data seem to indicate that at least one change of vector is necessary for the maintenance of the virus cycle. Mosquito-borne viruses would have to undergo a first cycle in those species which are prevalent in spring, particularly those of forest, but in early summer change to other species (mainly *Ae. vexans*) which do not occur in forests but are abundant in meadows.

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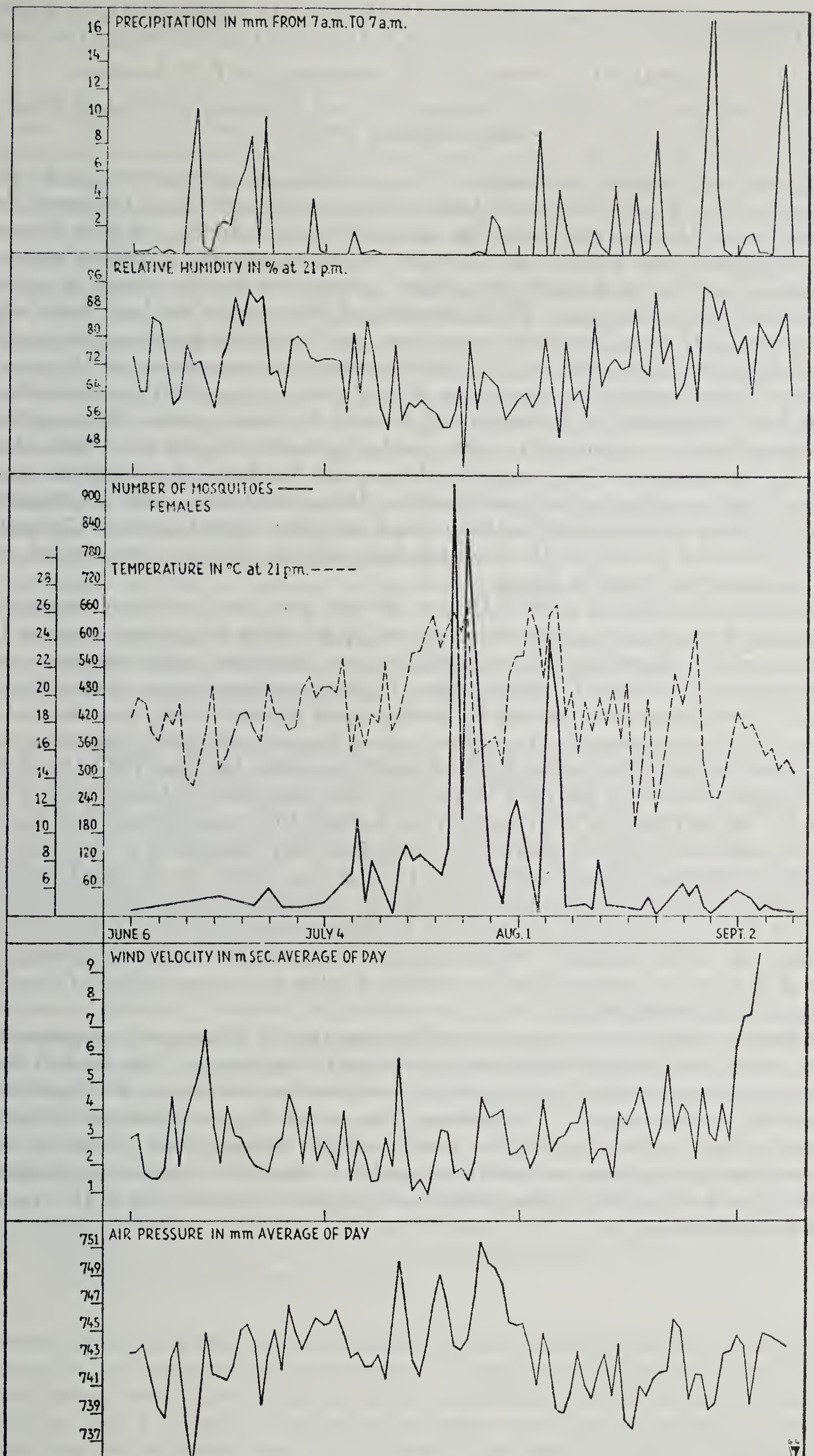

Fig. 2. Influence of major meteorological factors on flight of mosquitoes to artificial light.

THE VECTOR POTENTIAL OF SEVERAL ORIENTAL MOSQUITOES BASED ON THE LABORATORY TRANSMISSION OF JAPANESE ENCEPHALITIS VIRUS

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Infections with Japanese encephalitis (JE) virus occur over a broad area of the Orient—from as far north as Siberia, Korea and Japan, southward through China, Okinawa, Formosa, the Philippines to Malaysia and Indonesia—and as far west as India. At least fifteen species of mosquitoes have been listed in the literature as either suspected or proven vectors of JE virus in one or another part of this vast region. It appears that the vector or vectors may vary from one area to the next. The implication of these species has been based either (1) upon recovery of JE virus from wild mosquitoes, or (2) epidemiologic association with outbreaks of Japanese encephalitis or, (3) the experimental transmission of JE virus in the laboratory. At the present time association of six of these species with the transmission of this virus has been established on the basis of all three of the above points: The mosquito *Culex tritaeniorhynchus* has been implicated over most of the known distribution of the virus; the closely related *C. gelidus* appears to be a vector in Malaya and Thailand; the temperate zone house mosquito, *C. pipiens pallens* has been implicated in Japan and China, while the tropical house mosquito, *C. pipiens quinquefasciatus* has been found naturally infected in South China; Chinese workers reported the recovery of JE virus from *Aedes albopictus;* finally, an anopheline, *Anopheles hyrcanus* is a suspected vector in Japan.

Investigations conducted at WRAIR over the past few years have been directed towards a comparison of the efficiency with which several of the above mosquitoes transmit JE virus in the laboratory. Experimental transmissions were attempted with colonized strains of *C. tritaeniorhynchus, C. gelidus, C. pipiens pallens, C. pipiens quinquefasciatus, Aedes albopictus* and *A. aegypti.* Mosquitoes were infected by feeding upon viremic chicks, and they were refed upon normal chicks at intervals of from three to forty days or more after their infectious blood meal. When the four *Culex* species ingested blood containing less than 100 LD_{50} of JE virus the transmission rates were less than 10 per cent after extrinsic incubation periods of 10 or more days. As the dosage of virus ingested was increased the transmission rates rose and the periods of incubation required shortened. Infections were established in *C. tritaeniorhynchus* and *C. gelidus* which had ingested less than 10 LD_{50} of virus, while the threshold infecting dose (concentration at which one per cent or more of the mosquitoes became infected) was between 10 and 100 LD_{50}'s for *C. pipiens pallens* and *C. pipiens quinquefasciatus*, and between 100 and 1000 LD_{50}'s for *Aedes albopictus.* With *A. aegypti*, a species that has not been implicated as a vector of JE virus, no transmissions were obtained unless the concentrations of virus ingested was greater than 10,000 LD_{50}'s .

We have recently begun attempts to establish the ID_{50} of JE virus for mosquitoes by feeding them upon viremic chick blood through artificial membranes. This method is quicker than that previously described since a series of concentrations of virus can be offered to groups of mosquitoes simultaneously. Furthermore, the use of ID_{50} is considered to be a more significant index of vector potential than is the threshold infecting dose. Thus far, using the membrane feeding technique, we have been unable to establish infections in *Armigeres subalbatus, Aedes togoi* and *Anopheles stephensi* which have ingested concentrations of JE virus ranging from 10 to 10,000 LD_{50}.

RECENT RESEARCH ON THE TRANSMISSION OF LEISHMANIASIS

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Sudan. The most comprehensive work has been done by the Kala Azar team of Namru-3 under the direction of H. Hoogstraal (1961-1963). *Phlebotomus orientalis* was proved to be the vector. It was found to be common in Acacia forest islands in an endemic Kala Azar area (Malakal), but absent in the open savannah and in villages in the savannah where *P. papatasi* was common. The natural infection rate determined by individual dissection was 1·9%. The behaviour of the flagellates was typical, the intensity of the infection was high (5,000-10,000 flagellates per fly) with heavy anterior concentrations and no parasites in the hindgut. The intensity of infection remained constant or increased with age. 33 (54%) of 61 hamsters inoculated with leptomonads from wild sandflies developed infections.

Comparison of the behaviour of a strain of Kala Azar in *P. papatasi* with that in naturally infected *P. orientalis* (Heyneman, 1963) gave the following important results: The infection rate in *P. papatasi* was about 100% on days 1 and 2, but fell to 15% on day 15. The intensity of infection fell from about 10,000 flagellates to about 100 per fly. Infection was intensive first in the midgut, while cardia and hindgut were invaded later. From day 5 there was rapid loss of flagellates, many of them dead or inactive, through the hindgut. Thus, presence of flagellates of *Leishmania* in the hindgut does not prove transmission by contamination, but presence in a sandfly other than the normal vector.

Transmission by bite and presence of flagellates in pharynx and mouth parts has not been shown so far.

Reservoirs: 227 dogs examined proved negative. *Leishmania* was found in 6 rodents of 3 species out of 242 rodents examined. This low figure makes it doubtful whether the rodents are the normal reservoir of human Kala Azar in the Sudan.

Kenya. Heisch, Minter *et al.* (1954-1963) proved that *P. martini* and perhaps 2 other related species are the vector(s). One *P. martini* was found naturally infected and a hamster inoculated became infected. This strain proved later infective for man. The behaviour of the flagellates was typical, with heavy anterior infections. The distribution of *P. martini* coincides with that of the disease. Hamsters inoculated with flagellates from other species of *Phlebotomus* did not become infected. A special feature of Kala Azar in Kenya is its connection with termite hills in which the sandflies rest. *P. martini* proved common in termite hills in microfoci of Kala Azar and was absent or very rare in control areas.

British Honduras. Lainson and Strangeways-Dixon (1962-1964) studied the reservoirs and transmission of cutaneous leishmaniasis. The natural infection rate in sandflies proved low (only 2 weak infections out of 334 sandflies examined), but inoculation of a pool of 270 wild caught sandflies produced an infection in a hamster. Experimental infections of sandflies showed heavy anterior concentrations of flagellates.

Reservoirs: 350 forest animals of 18 species were examined and *Leishmania* was found in 15 rodents of 3 species out of 86 rodents examined. Infections were purely cutaneous, on the tail only. 3 transmissions by inoculation of rodent strains to humans were successful. 5 of 10 men trapping rodents in the forest became infected. The authors conclude that there are probably different species of *Leishmania* in forest animals, some of which may not be infective for man. The disease is definitely a zoonosis.

Panama. Hertig, Johnson and McConnell (1963) studied the behaviour of flagellates in experimentally and naturally infected sandflies. There were hindgut infections from day 3 with short forms and rosettes adhering to the epithelium. Infections of the cardia were observed from day 4. Heavy infections of the cardia were seen in *Lutzomyia gomezi* in 55% on days 4-7 and in 94% after day 8. Six out of 47 infected *L. gomezi* had flagellates in the pharynx. Natural infections varied from 2 to 15·4% according to species and locality. Infections were always in the hindgut and the malphigian tubes, less than 5% in the cardia.

The strains have not been identified, but human leishmania strains are probably included. 2 strains isolated from sandflies produced lesions in hamsters like those produced by human strains. These strains produced heavy anterior infections in sandflies. Precipitin tests with sandfly strains against human antiserum were negative. Only 4 strains of 17 isolated from sandflies and inoculated into hamsters gave infections. (Human strains give 100% infections). The majority of the sandfly strains is apparently not infective for hamsters. Presence of leptomonads in sandflies thus does not necessarily prove them vectors of human leishmaniasis.

RUSSIA. Shoshina (1953) concluded after dissecting several *S. arpaklensis* with hindgut infections and observing the exit of flagellates from the anus that infection by contamination is possible. As shown above, hindgut infections occur when flagellates of *Leishmania* are not in their normal vector and do not prove infection by contamination.

Statements in the Russian literature that a species of *Phlebotomus* is a vector of leishmaniasis are generally based on epidemiological data or on infection rates with flagellates. There seem to have been no attempts to identify the parasites or transmission experiments (except for an experiment of transmission of *Leishmania tropica* by *P. papatasi*, Kryukova, 1941). Infection rates of *Phlebotomus* of 5 to 48% are given. Belova (1963) did not succeed in infecting mice with cultures of flagellates from *P. caucasicus* and Shuikina (1962) distinguished various types of flagellates in sandflies, some of them not leptomonads. Both authors conclude that there are flagellates in sandflies which are not infective for man. The high infection rates given and statements that a species of *Phlebotomus* is a vector need confirmation by experimental work and the identification of the flagellates.

THE TRANSMISSION BY *CHRYSOPS* SPP. (DIPTERA) OF THE HUMAN AND SIMIAN STRAINS OF *LOA*

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In the rain-forest zone of the Cameroons infections with *Loa loa* are found in the human population and show a diurnal microfilarial periodicity. The prevalence of microfilariae carriers varies according to the situation of the village examined and the age of the population, but is not usually higher than 30 per cent. The numerical density of microfilariae in the blood of human cases if often high (50-1000 per 50 cu. mm.) and in the individual it may remain at a high level for many years.

Under experimental conditions the drill (*Mandrillus leucophaeus*) can be infected with the diurnal human parasite. In the monkey host the parasites are of small somatic size but the microfilariae retain their diurnal periodicity.

Under natural conditions in the rain-forest surrounding human habitation infections with *Loa* are found in three species of monkey (*M. leucophaeus*, *Cercopithecus nictitans martini*, and *C. mona mona*), but in all infections so far examined the adult worms and microfilariae have been of large somatic size and the microfilariae have exhibited a nocturnal periodicity. In the drill, which is the main host for the natural simian strain of *Loa*, over 90 per cent of the population show adult worms and microfilariae at autopsy, but it is characteristic of all infections with *Loa* in monkeys that after the first few weeks of the infection the spleen begins to exert a suppressive action on the numbers of microfilariae in the peripheral blood and maintains them thereafter at very low levels (5-20 per 50 cu. mm.), despite reinfection with either strain of parasite, throughout the duration of the infection. The monkey population in nature thus shows a high proportion of infected individuals carrying small numbers of available microfilariae exhibiting a nocturnal periodicity.

The divergent evolution of the human and the simian *Loa* complexes can be correlated with the biting habits of their respective *Chrysops* vectors. *C. silacea* and *C. dimidiata* (Bombe form) are the vectors of the human parasite. They are found at all levels in the forests but

they are readily attracted to ground level and will leave the forest to enter villages and houses They are attracted by wood smoke and feed readily on man. The infection rates recorded in these species are usually of the order of 3-5% and the mean number of parasites per fly is usually around the high figure of 80. Of 20 flies carrying naturally acquired infections all gave rise to diurnal infections when inoculated into monkeys. These observations taken in conjunction with the fact that these species bite only during daylight hours suggests that they obtain their blood-meals mainly from man.

The vectors of the natural simian parasite are *C. langi* and *C. centurionis*, two species which begin to bite just before sunset and continue into the early hours of the night. They are only taken biting at canopy level in the forest and it is presumed that they are feeding on sleeping monkeys. The infection rates in these species are high (12-32%) but the number of parasites per infected fly is low (16-26), and the parasites carried by three *C. langi* and two *C. centurionis* all gave rise to nocturnally periodic infections when inoculated into experimental monkeys. All these observations are compatible with the assumption that both species obtain their blood-meals from monkeys.

Despite the observed divergent evolution of the two host-parasite-vector complexes described above the possibility of exchange of parasitic material between them still exists and we may speculate as to why such transference is scarcely detectable.

Transference of the simian parasite to man has never been successfully achieved under experimental conditions nor have natural human infections with the nocturnally periodic strain ever been detected. The crepuscular canopy-dwelling vectors of the nocturnal parasite never come into contact with man under normal circumstances, while any *C. silacea* or *C. dimidiata* which succeed in feeding on monkeys by day are most unlikely to ingest microfilariae of the nocturnal strain.

Transference of the human parasite, via *C. silacea* or *C. dimidiata*, to monkeys in the forest is a more likely occurrence. It is suggested, however, that these species find it difficult to obtain blood meals from monkeys when they are active and awake. The parts of the monkey body which are devoid of protective hair are limited to the face, extremities and buttocks, and observations on captive drills in the forest lead us to believe that it is often the monkey which catches the *Chrysops* and eats it before the fly can succeed in biting.

Another factor concerns the characteristics of the hybrid strain of *Loa* which results from cross-mating the diurnal and nocturnal strains. Such cross-mated females produce scanty microfilariae and do not remain fecund for long periods. Furthermore they produce microfilariae of a characteristic but predominantly diurnal periodicity in which microfilariae persist in the peripheral blood no longer than 9 p.m.

In nature the occasional diurnal parasites that are cyclically transmitted from man to monkey will be likely to encounter a host already infected with the nocturnal strain of *Loa*. The diurnal males will thus find few unfertilized nocturnal females with which to mate, while the diurnal females will in all probability be fertilized by the mature nocturnal male worms already present. The resultant microfilariae of the hybrid strain will be scanty, of predominantly diurnal periodicity, and will be subjected to the suppressive action of the spleen. It is thus improbable that they will be readily available for further transmission by the crepuscular vectors.

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ON THE FAMILY INFECTION OF BANCROFTIAN FILARIASIS IN JAPAN

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During many years of filariasis survey in Japan, we have found that, in some cases, there exist remarkable differences in endemicity between neighboring villages and among houses of the same village.

In Japan, Bancroftian filariasis is widely distributed in southern parts and in the Ryukyus. About ten mosquito species are susceptible to *Wuchereria bancrofti.* Among these, the house mosquitoes, *Culex pipiens pallens* in Japan and *C. p. fatigans* in the Ryukyus are the commonest and highest in natural as well as experimental infection rates.

As has been reported by the author, the mosquitoes are highly domestic and breed in domestic foul water such as sinks, sewers, drains, and earthen jars containing foul water or diluted night-soil near houses; and in some cases, fertilizer pits in the fields around the village. They are strongly anthropophilic in feeding habit. Their hiding places are around barns, under bushes and in the undergrowth of thickets near houses. They also have a tendency to rest in houses.

Observations show that the natural infection rate is highest in mosquitoes caught early in the morning within mosquito-nets where a family including one or more carriers have spent a night. The rates are fairly high in mosquitoes found within carriers' houses in the morning or at night, while, in mosquitoes captured in places free from carriers, even when they were caught near carriers' houses, natural infections are scarcely found. This implies that transmission of the disease might be taking place more actively in close proximity of sleeping sites of carriers.

Because of the very domestic feeding, breeding and resting habits of the vector mosquitoes, prevalence of Bancroftian filariasis in these areas seems to be in a form of familial infection.

When groups of houses are isolated by barriers such as valleys, cliffs, groves, bamboo thickets, or thick, high hedges, then patch type distribution of filariasis may take place in a village, according to the number of carriers and the presence of favorable breeding places for the vectors. This may be true between neighbouring villages also. Generally, however, familial infections and localization of infections cannot be proved significantly, especially in villages of low microfilarial incidence, because the houses are usually roughly grouped together and there are not barriers sufficiently thick as to hinder mosquito flight within the village, and because carriers of younger ages often leave their families to marry or emigrate.

RELATION BETWEEN VIRUSES AND TICK TISSUES *IN VITRO*

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Ixodid ticks are known to be vectors and reservoirs of viruses, rickettsiae and Protozoa. It is interesting to study the relationship between these micro-organisms and tick tissue *in vitro* as a preliminary to the study of many important questions, e.g. preparation of a suitable substrate for isolation and culture of micro-organisms, inter-relationships of different micro-organisms in tick tissues, or their classification, etc.

The present report concerns the relationship between several viruses and ixodid tick tissues *in vitro*, for which the fundamental requirement is the elaboration of suitable tissue culture. We have succeeded in preparing tick tissue cultures and this enabled us to perform the experiments. In order to establish the relative sensitivity of the tick tissue to viruses, twenty-two different viruses were used. Arboviruses belonging to the group A (EEE, WEE, Semliki and Sindbis) readily multiplied in this substrate; the tick-borne viruses from the group B (European tick-borne encephalitis, Russian spring-summer encephalitis, Omsk hemorrhagic fever, Kyasanur Forest disease, Powasan and louping-ill viruses) multiplied equally well but Langat (TP 21) virus multiplied very poorly. The virus titre increased by approximately

0·5-1 log. unit per day and, using small doses of viruses as inoculum, it reached 10^5 infectious doses by the 8th day after inoculation. No cytopathic effect caused by the propagation of viruses was ever noticed. The other viruses from group B (Japanese B encephalitis, West Nile, St. Louis and yellow fever viruses) which are transmitted in nature by mosquitoes also multiplied in the system employed but the titres obtained did not exceed 10^3 infectious doses. Viruses not belonging to any of known arbovirus groups (polio, vaccinia, pseudorabies, Newcastle disease, encephalomyocarditis and vesicular stomatitis) did not multiply; but the virus of lymphocytic choriomeningitis multiplied very well.

More attention was paid, however, to the viruses which multiplied in tick tissue cultures. Among these, the European tick-borne encephalitis virus was chosen for detailed studies. The relationship between this virus and tick tissues was studied from two points of view.

A comparison has been made of the susceptibility of tick tissues and chick embryo cells, which are known to be sensitive substrates for the cultivation of tick-borne encephalitis virus. It was shown that with inocula of 0·3 and 0·03 IfD_{50} (50 per cent interference dose) the respective percentage of infected cultures was 76 and 18 with tick cells and 36 and 3 with chick embryo cells. Thus, tick cells appear to be more sensitive for detection of small doses of tick-borne encephalitis virus.

The presence of tick-borne encephalitis virus in tick cells has been studied by means of fluorescent antibody staining. The preliminary results have shown that virus propagation occurs only in the cytoplasm and was concentrated around the nucleus.

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THE INCIDENCE OF ARTHROPOD BORNE VIRUSES IN AUSTRIA

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In virological and serological investigations we have proved that the tick-borne encephalitis (TBE) virus has been present in the eastern part of Austria, at least since 1927. In 1956, we started a special continuous investigation of this virus. All patients suffering from diseases of the central nervous system (CNS) were examined by clinical, epidemiological and virological-serological methods. Up to now, we have obtained results indicating that the virus is mainly distributed in the eastern and south-eastern parts of Austria, but we have also proved the existence of human cases of tick-borne encephalitis (TBE) as far west as the border of Western Germany in Upper Austria.

In a previous examination of different sera from residents of four districts of Austria, haemagglutination inhibiting (HI) and neutralising (NT) antibodies were discovered against several arboviruses (1). We can conclude that at least one mosquito-borne virus, the Tahyna-virus, occurs in some areas of the country, an assumption supported by the following facts:

1. The isolation of the virus in the neighboured Slovakia by Bardos and Danielova, and 2. the high incidence of antibodies among residents of Klosterneuburg, a suburb of Vienna on the Danube. We have, since 1961, concentrated our investigations on this Tahyna-virus. For this study, we collected sera from forest-workers whom we had examined first for the NT against TBE virus. We were able to prove that the standardised infection rate of forest-workers with TBE virus is about three times higher on the average than that among the other residents in an endemic district.

These sera of the forest-workers were again used for the HI-test against 6 antigens. We have examined up to now 849 sera, and we have obtained some preliminary results. We may assume that reactions with antigens on Murray Valley encephalitis and West Nile are to be interpreted as cross reactions among the group B, because most of the persons also possessed antibodies against TBE virus. The number of antibodies against group A and Bunyamwera viruses is too slight to allow us to draw a conclusion. But the high number of antibodies

against Tahyna-virus is striking. This becomes yet more evident if one compares the geographic region of the origin of the sera, and here one can see that the highest rate of antibodies occurs in areas east of Vienna on the Danube river.

This is in a good accord with the optimal conditions of breeding places of *Aedes vexans* mosquitoes. But, all trials in order to isolate this virus from mosquitoes or by the sentinel mice technique have failed in the past years.

Besides that, we have also attempted to isolate the virus from the blood of human beings with a simple feverish illness. Tahyna-virus was never isolated from these specimens. However, we succeeded in isolating a TBE virus from a soldier with a fever. In the NT with paired sera, however, we could prove antibodies against Tahyna-virus in 13 out of 51 patients examined. In one case, a conversion from the first serum on May 27 to the second sample on June 5, 1963, was found. This means that this virus must have also been present in Austria in the summer of 1963, though all our trials to isolate it failed. In this year 1964, we are continuing this work, concentrating on attempts at isolating the virus from mosquitoes.

(Since writing this, we have isolated Tahyna virus from *Aedes* caught east of Vienna.)

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QUANTITATIVE FIELD-STUDIES ON THE CYCLE OF TICK-BORNE ENCEPHALITIS IN A FOCUS IN LOWER AUSTRIA

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Since 1961 field investigations have been carried out in a focus of TBE near Pottschach in Lower Austria. Studies on the mouse population with regard to the host-vector-relation have shown that the larvae of the ticks almost always feed on mice and the mice form a basic cycle of TBE with tick larvae and nymphs.

In attempting to obtain more exact data on population density and age structure of the mice as well as on infestation with ticks and incidence of infection we enlarged the area of mice-control from 1/3 ha. to 1 ha. and instead of a three weeks' interval, a two weeks' interval of two nights trapping with 40 feeding stations instead of 15. The captured mice were anaesthetized to allow a continuous study of living mice and their infestation by ticks.

In autumn, blood was withdrawn by heart aspiration from the mice in the field and the serum was tested for neutralizing antibodies against TBE.

Within the same area hungry stages of ticks were collected in 32 fields of 16 m² each at a three weeks' interval. 4,136 larvae, 4,660 nymphs and 229 adults were caught in 512 m² within the focus. 148 mice (*Apodemus flavicollis* and *sylvaticus*, *Clethrionomys glareolus* and *Microtus agrestis*) were marked and released. 224 retrappings succeeded. The average rate of infestation with ticks was 18·5 larvae and 0·43 nymphs per mouse. Mice, infested with nymphs, had an average of 30 parasitizing larvae.

From 53 mice, heart aspirated in autumn, 2 had neutralizing antibodies aginst TBE (i.e. 4%).

On this base we assumed that in 1 ha. of our focus in 1963 more than 100,000 larvae, 80-90,000 nymphs and 3,500-4,500 adults were active. 60,000-70-000 larvae and about 1,400 nymphs may have parasitized mice. The relation between active and parasitizing tick stages shows that the majority of the larvae feed on mice but only 1/4 of the nymphs.

If 4% of the mice living on 1 ha. are infected, it can be estimated that about 2,000 larvae receive the virus from them. If 1,000 of them were active as nymphs, we should have a contamination rate of 1 per thousand. This is the rate found in 1961 and 1962. On the other hand, it can be assumed that from 60 larvae, feeding on a viremic mouse, 1 has the chance of infecting another mouse in the nymphal stage.

Finally, it can be estimated that in this focus the ecologic conditions allow mice to play the main role in the cycle of TBE.

DEVELOPMENT OF *COXIELLA BURNETI* FROM THEIR ULTRAFILTERABLE PARTICLES IN TICKS *IN VIVO*, THEIR ORGANS *IN VITRO* AND IN TICK TISSUE CULTURES

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Filterable particles of *Coxiella burneti* present in suspensions of yolk sacs of infected embryonated hen eggs were found to pass through collodion membranes with a mean porosity of less than 100 mμ. Considering that the minimal size of elementary bodies of *C. burneti* is 250×300 mμ, then the size of the filterable particles is approximately 10 fold smaller. From these ultrafilterable particles, after a certain time of cultivation, agents develop which do not differ in their morphological and antigenic properties from typical *C. burneti*. Antigens could not be prepared from filtrates of *C. burneti*, and guinea pigs inoculated with filterable particles did not produce detectable antibodies. Thus, antigenicity and immunogenicity seems to be confined to mature organisms only. One could assume that the filterable particles represent material at an early stage of intracellular development of *C. burneti*.

Recently, investigations were made to demonstrate the eclipse phase of *C. burneti* cultured in different cell lines (1). The results indicate a significant decrease in infectivity during early stages of infection followed by a marked increase later on. The decrease is remarkable in cells in which *C. burneti* multiplies well, but is rather insignificant or does not occur in cells in which it simply survives.

To obtain more exact information on the behaviour of *C. burneti* in cells, ultrathin sections of infected tissues were examined by electron microscopy (3, 4).

Even in the case of a high multiplicity of infection, no *Coxiella*-like particles were found in either the cytoplasm or nucleus during the first hours after inoculation. In the cytoplasm of infected, as distinct from normal cells, there appeared broad areas of fine granular structures varying in size.

In such smaller areas we observed concentrations of dense material and also aggregates of large dense granules. At 48 hours after infection there was no morphological evidence of *C. burneti*-like particles multiplying by binary fission. We assume that these areas, which we called matrices, could represent the basic material from which mature *C. burneti* could be formed by further differentiation. Considering that the fine granular material of the matrix may represent a nucleic acid-containing substance, then the possibility cannot be excluded that these materials can become infectious.

Because ixodid ticks constitute a very favourable medium for cultivation of *C. burneti*, we inoculated specimens of *Ixodes ricinus*, *Dermacentor marginatus* and *Haemaphysalis inermis* with a suspension of ultrafilterable particles of *C. burneti*. Morphologically and antigenically typical organisms were regularly observed in their tissues from the 4th day on.

In the cells of the haemolymph and tissues of various organs morphological changes were observed which we considered directly connected with the development and multiplication of *C. burneti*. Thus our observations indicate that ticks are suitable media for cultivation and detection of these filterable forms of *C. burneti*. In this connection it is worthwhile mentioning that many authors have reported insects infected with the agent of Q fever without detecting the rickettsiae microscopically. These findings may be explained—at least to some degree—by the existence of ultramicroscopic "immature" forms of *C. burneti* as indicated by our observations.

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RECHERCHES SUR LES ESPECES DE PHLEBOTOMES EXISTANTS DANS LA NATURE EN ROUMANIE

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Les captures ont été effectuées (*a*) à l'aide de pièges de papier collant, placés pendant la nuit dans les abris naturels ainsi qu'à l'extérieur des habitations et (*b*) à l'aide des éprouvettes utilisées pendant la journée à l'intérieur des habitations et soir et matin près des abris naturels.

Phlebotomus (*Phlebotomus*) *papatasii* Scopoli 1786 a été capturé dans les régions de Banat, Olténia, Bucarest et Dobroudgea, surtout à l'intérieur des maisons (chambres à coucher) et rarement à l'extérieur, sous les auvents.

Phlebotomus (*Larroussius*) *major* Annandale 1910 a été identifié: (1) dans les roches granitiques des monts Măcin de la Dobroudgea jusqu'à une altitude de 350-400 m.; (2) dans les nids d'oiseaux des berges sablonneuses le long du Danube, au Banat; (3) associé à *P. perfiliewi* dans les nids d'oiseaux des berges, en Olténia, près de Turnu Severin; (4) associé à *P. chinensis var. simici* dans les grottes superficielles et les fissures des roches des berges calcaires et arides du défilé du Danube.

Phlebotomus (*Larroussius*) *perfiliewi* Parrot 1930 a été identifié en Olténia dans des nids de *Merops apiaster* et de *Citellus citellus* des berges sablonneuses situées dans une région de vignobles et de vergers.

Phlebotomus (*Adlerius*) *chinensis var. longiductus* Parrot 1928—un seul exemplaire mâle, capturé dans un nid de *Merops* d'une berge tout près du Danube au Banat, où *P. major* était aussi présent.

Phlebotomus (*Adlerius*) *chinensis var. simici* Nitzulescu 1931 a été identifié dans une région de Banat, qui coïncidait en grande partie avec la région peuplée par *P. major;* de même il a été capturé dans les ruines des anciens châteaux forts de Svinita, Ada-Kaleh, Tr. Severin.

Phlebotomus (*Paraphlebotomus*) *alexandri* Sinton 1928 a été capturé en 1961 et 1963 dans les grottes et les fissures des berges calcaires, d'une ancienne carrière de pierre, située tout près du village Ion Corvin, en plein plateau de la Dobroudgea.

Dans nos recherches la densité phlébotomienne a été généralement réduite, 1 à 6 exemplaires par nid ou fissure de roches. En même temps, la densité de *P. papatasii* dans les habitations avoisinantes a été souvent assez élevée (40-80). Il est à remarquer que dans le foyer de leishmaniose en Olténia, la densité de *P. perfiliewi* a été nettement supérieure (Lupaşcu et collab., 1955) atteignant 159 exemplaires pour un nid de *Merops apiaster* et que dans les mêmes endroits l'espèce est devenue rare les années suivantes.

Les mâles ont prédominé dans les captures de nuit (70 à 100%) tandis que les femelles ont prédominé parmi les exemplaires capturés à l'éprouvette pendant leur vol, matin et soir, tout autour des abris.

On a rarement constaté l'approche des espèces de phlébotomes sauvages des habitations humaines. Nous avons capturé pendant la nuit de manière sporadique les espèces *P. major*, *P. chinensis var. simici* et *P. perfiliewi* (1 à 2 exemplaires) à l'extérieur des maisons. Seulement *P. perfiliewi* a été identifié aussi à l'intérieur des maisons dans le foyer de leishmaniose mentionné. *P. chinensis var. longiductus* a été capturé antérieurement en Roumanie dans les villes de Bucarest et Jassy et toujours dans les maisons (Nitzulescu, 1929,1937).

Nous considérons à la suite de ces recherches que les espèces appartenant aux sousgenres *Larroussius*, *Adlerius* et *Paraphlebotomus* représentent des espèces sauvages dans les conditions climatiques de notre pays, qui situé à la limite nordique de l'aire de distribution de ces insectes détermine probablement une délimitation écologique plus stricte de ces espèces. Ces espèces peuvent exercer leur rôle de vecteur soit dans les abris naturels ou dans leur proximité.

REARING FLIES FROM FAECES AND MEAT, INFECTED UNDER NATURAL CONDITIONS

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For studying the question of food and breeding media of synanthropic flies regular collections with fly traps baited with human faeces and meat were made in three localities in Hungary. The baits were later taken to the laboratory for breeding.

Out of the 31 faeces-baits 2,702 flies were reared. The dominant species was *Parasarcophaga albiceps* with 1,160 specimens (42·9%). Other important species were: *Bellieria melanura* 605 (22·4%), *Nemopoda nitidula* 360 (13·3%), *Coprosarcophaga haemorrhoidalis* 173 (6·4%), *Ravinia striata* (6·3%). The rest consisted of *Pegomyia socia*, *Sepsis punctum*, *Hylemyia strigosa*, *Myospila meditabunda*, *Hydrotaea dentipes*, *Piophila foveolata*, *Fannia canicularis* and *Paregle cinerella*.

Of the 31 baits yielding flies by rearing, 24 were also used in fly-traps. Among others a great number of *Lucilia* and *Calliphora* imagos were caught on them. *Lucilia caesar* was predominant with 725 specimens. The five other *Lucilia* species gave 124, the two *Calliphora* taxa 99 specimens. Nevertheless not a single specimen was reared. Their breeding in faeces seems improbable, and either happens very rarely or such data derive from erroneous observations.

The meat baits, usually pork, gave 2,864 flies from 27 baits. Most of them, 1,287 (44·9%) belonged to *Lucilia sericata*. Next stands *Parasarcophaga scoparia* with 497 specimens (17·4%) Other species are: *Piophila foveolata* 10·7%, *Ophyra leucostoma* 10·6%, *Calliphora erythrocephala* 9·6%, under 2% were *Lucilia ampullacea*, *Muscina pabulorum*, *Lucilia caesar*, Milichiidae (*Meoneura* sp.), *Parasarcophaga similis*, *Fannia canicularis*, *Tricimba cincta* (Chloropidae?), *Azelia* sp., *Piophila latipes* and *Lucilia illustris*.

On a series of experiments the baits were exposed for 1 to 7 days. The rearings on meat showed that the dominant *Lucilia sericata* was nearly completely suppressed by the viviparous *Parasarcophaga scoparia*. In baits in which *Ophyra* larvae developed, *Parasarcophaga scoparia* was also annihilated. Only *Piophila foveolata* could outlive the *Ophyra* invasion. There was no significant difference between the baits exposed for a different number of days.

The same experiments were made with faeces. The ratio of species after a longer exposure showed no difference against those exposed for a few hours only.

The rearing experiments gave also the period of development and succession of the species breeding in faeces and meat. The life-history table of *Parasarcophaga albiceps* shows that all larvae can finish their development if they are laid before the middle of July. Larvae laid later, between the middle of July and the end of August, give some flies in about three weeks, but a part of the puparia overwinter. Larvae laid after September 1 yield flies only next year. Concerning *Bellieria melanura* we have less data, but adults developed from larvae laid up to the middle of August; only a part of them developed from September larvae, and all went into diapause from larvae laid after the middle of September. *Lucilia sericata* fully developed from eggs laid up to 16 August, but went partly to hibernation from eggs laid later.

The time needed for the hatching of the flies from faeces also differed. *Sepsis punctum* needed the shortest, *Parasarcophaga albiceps* the longest time for emergence.

The rearing of flies from media infected under natural conditions may give a deeper insight into the ecology of synanthropic flies. As only a part of the experiments discussed were made in villages and human habitations, in the future more investigations should be made to study flies visiting and developing in cesspools which are probably the most dangerous sources of infection.

HIGHER DIPTERA

THE MAINTENANCE IN THE LABORATORY OF A COLONY OF *GLOSSINA MORSITANS* (DIPTERA) SINCE 1959

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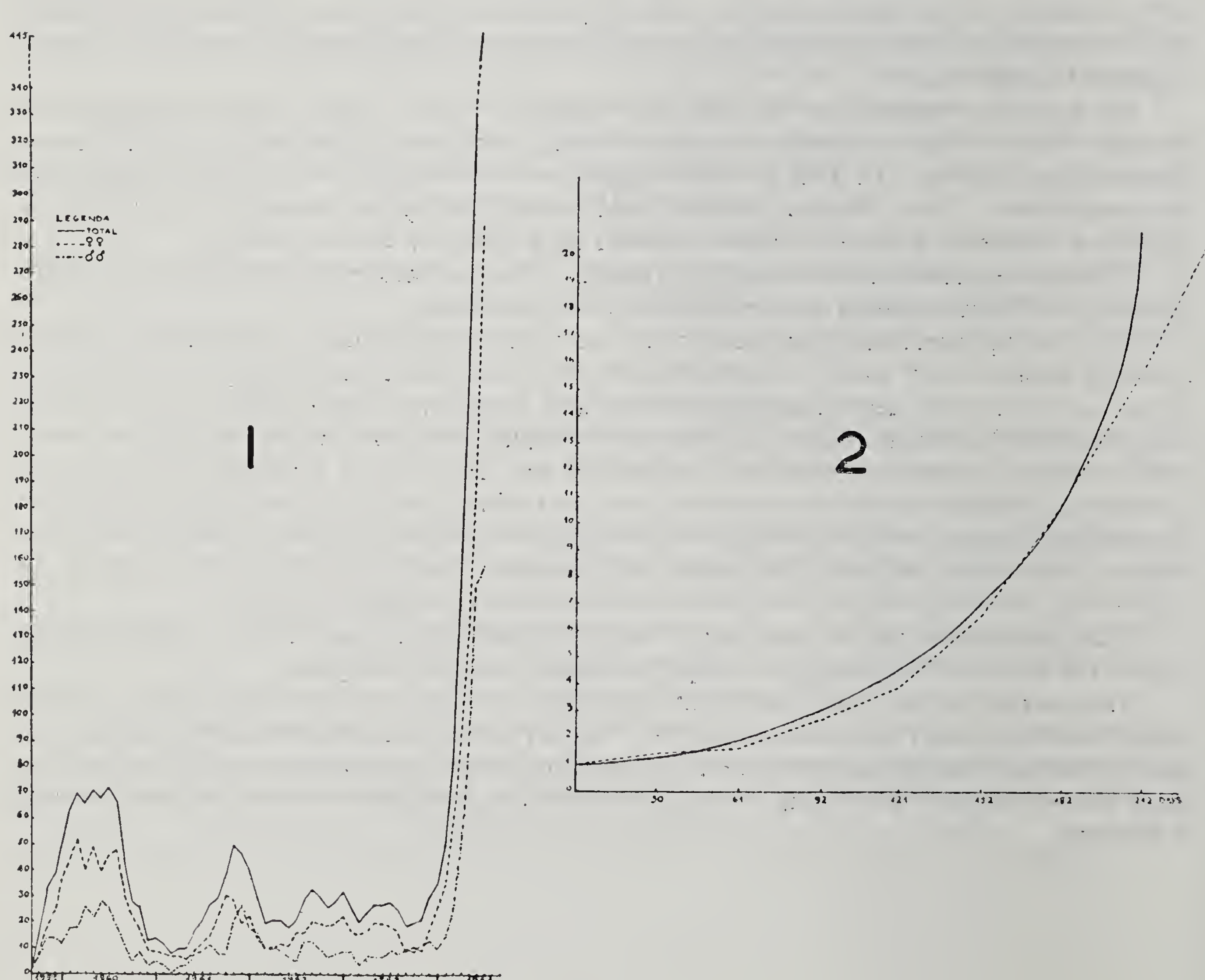
Breeding of *Glossina* has been attempted in Africa, thus in an adequate climate environment, and in Europe, i.e., in an artificial climatic environment. We tried in Lisbon in 1959 to breed a strain of *G. morsitans* from 65 Mozambican pupae which produced 45 adults, and which was maintained for 115 days, corresponding to three generations; however, we were unable to get more than a total of 45 adults simultaneously. Attempts have been resumed and this is an account of the results obtained up to the present.

Origin of the insects: We started with 43 glossinae—21 males and 22 females—born in our Laboratory between 14th October and 6th November 1959 from 4 lots of pupae sent by air from Govuro (Mozambique) in September 14 and 24, and October 1 and 22, 1959, through the kindness of Dr. Santos Dias of the Mozambican Trypanosomiasis Combat Mission.



Figs. 1-2. (1) Evolution of the laboratory population of *Glossina;* (2) probable evolution of an ideal population according to Buxton (solid line), compared with the laboratory population (broken line).

Environmental conditions.—We used an environmental chamber, 3 m. long, 3 m. wide and 2·5 m. high, with temperature and humidity set respectively to 26°C and 70% R.H. with fluorescent lighting at 550 lx during day-time. An automatic switch turned the lights on at 6 a.m., and off at 6 p.m.

The adults are kept in Roubaud-type cages made of a wire frame lined with cloth, 14 × 8 × 5 m., covered with a tulle cloth sleeve with meshes of approximately 2 mm. The cages are placed on two glass supports inside glass tanks thus leaving a space under the cage so that the larvae may come out. The glossinae are isolated from each other except during 2-3 days when a couple is put into the same cage for mating.

Initially, the pupae were kept in the open air, in small glass tubes—covered with netting. At the end of 1963, the pupae were placed in wet sand the moment they were collected, i.e., less than 24 hours after formation, at first, using the devices of Parrot and Ribeiro for rearing *Phlebotomus*. We noticed, however, that the same results could be obtained by saturating with water any common sand with particles ranging from 0·15 mm. to 0·30 mm., draining some and then placing it into a small tube 8 × 3·5 cm. which was covered with tulle cloth.

Guinea-pigs were used as sole food source. The glossinae were fed with the help of the excellent apparatus devised by Geigy and in which the glossinae were placed during 20-30 minutes every day except Sundays.

Evolution of our population.—Fig. 1 shows the evolution of the population in number of insects at the end of each month, the 43 with which we started constituting the *first* generation. We have now reached the 25th generation. The marked rise shown on the graph, which started on November 1963, corresponded to the appearance of the 17th generation, of which some individuals are still living and coincided with the utilisation of wet sand for the pupae. Thus, at present, elements of nine generations—from the 17th to the 25th—are coexisting in the population.

Fig. 2 shows the evolution curve of the population in comparison with Buxton's theoretical curve. It may be noticed that the population's increase coincides with Buxton's calculations since, after 128 days, the population has increased to a little less than 5 times its initial size and after 175 days it had increased to a little more than 10 times that number.

Conclusions.—According to the results obtained, expressed first by the maintenance of a *G. morsitans* population in the laboratory for 5 years without introducing any individuals from the outside and because the colony shows no signs of degeneration we believe we may have the solution for an indefinite laboratory breeding of *G. morsitans*, with all its subsequent advantages.

TECHNIQUES FOR FEEDING BLOOD-SUCKING INSECTS ON LARGE LABORATORY ANIMALS, AND FOR THE DESPATCH OF INSECTS BY AIR FROM THE TROPICS

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A goat or sheep is led on to a trolley and is secured by a clip on its collar to a cross-bar below its neck and by a yoke-bar above; it is prevented from backing out by a chain which passes round the rump. N.B. The legs are not tied. The restraining rails and rods can be readily adjusted to fit different sized animals. The design permits of free access to all sides of the body for the application of insect cages, after the animal has been wheeled into the laboratory.

Four cages, of 1·8 kg. total weight, are secured to the beast by a single strap, which can be used for animals ranging in weight from 23 to 68 kg. The strap is made of stout elastic belting. A length of "male" Velcro is sewn to the top surface of one end of the strap, and a similar piece of "female" Velcro to the under surface of the opposite end. When the strap is stretched round the animal and cages and the two Velcro surfaces pressed together, the cages are securely held; when the insects have fed through the gauze-fronted cages, the two ends of the strap can be torn apart.

These techniques have proved most successful when feeding colonies of *Glossina austeni* on goats, and have been described in detail (Ann. Trop. Med. and Parasit., June 1964, 58).

A box and packing material have been devised for the transport by air of pupae from the tropics. The box, made of 3·8 cm. thick expanded polystyrene, is shock absorbent, very light and strong, and provides good insulation. The packing material for the pupae consists of a bottom and top layer of moist plastic foam, enclosing nylon shavings from a nylon rod turned down on a lathe. If pupae are poured on to such shavings, gentle shaking makes them lodge in the shock-proof coils. Packing materials reduce the volume of enclosed air by only 7%. Tests with laboratory-bred pupae of *Glossina palpalis* suggest that 400 can be enclosed for 4 days without impairment of emergence rate.

If the wrapped package is placed in a refrigerator at about zero it takes 5 hours for the internal temperature to drop from +18°C to 0°C, or in an oven, at 45-46°C, 3 hours for the temperature to rise from 20°C to 41·5°C. Performance can be considerably improved by including a thermo-stabilizer in the form of a water bag.

Evaluation by emergence rates from wild pupae is difficult because the percentage dead on collection is unknown. The mean emergence rate from over 11,000 pupae of *G. austeni* sent from Zanzibar (average travel time 3 days) was 60%, but batch rates up to 90% have been recorded.

For a detailed description of this work, see Ann. Trop. Med. and Parasit., Sept. 1964, 58.

EPIDEMIOLOGICAL IMPLICATIONS OF TWO SURVEY TECHNIQUES OF RECORDING THE OCCURRENCE OF *GLOSSINA* SPECIES

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Tsetse records from Ghana obtained between 1951 and 1955 show considerable epidemiological implications when records obtained by different survey techniques are assessed.

Distribution of tsetse. Nine species of *Glossina* were recorded in various localities of Southern Ghana. Table 1 lists localities showing new records i.e. not listed by Potts (8) and Buxton (1). These records were obtained almost entirely by traps (4).

In general, old records were confirmed, but in several localities surveys with traps located *G. pallicera* and species of the *fusca* group previously unrecorded. Some old records were not confirmed due possibly to the short period of my surveys, a change of tsetse distribution, inaccurate mapping, and possibly misidentification.

Ratio of species and sexes. Using some Kumasi and Ankaful records Morris (5) shows that ratios of species and sexes obtained by traps and fly-boys differ. Table 2 gives further examples to support this.

The species ratios in traps show the importance of not using man bait for recording the incidence of animal trypanosomiasis vectors. Traps provide a good, easy to work, substitute for the reliable but cumbersome animal bait. As expected female percentages in traps are higher than those obtained by fly-boys. Females of *G. palpalis* and *G. morsitans* live nearly twice as long as males (3, 6), so one would expect about 66% of females in tsetse populations, a percentage similar to that recorded by traps.

Age of tsetse in samples and infection rates. Age-grouping (9) of tsetse obtained by the two survey techniques shows that traps catch a higher proportion of older flies than do the fly-boys. Older flies have been shown to be more highly infected (1, 2). My dissections of 146 *G. morsitans* in Mokwa, N. Nigeria in 1956 showed the same trend:

78 Ag II flies	26·9% *vivax*	6·4% *congolense*	0% *brucei*
68 Ag III flies	23·5% *vivax*	8·8% *congolense*	4·4% *brucei*

It was possible to calculate the infection rate of the local *G. morsitans* population and this was: 10·3% *vivax*, 3·1% *congolense*, and 0·9% *brucei*. However, such calculations are only of comparative and not absolute value since samples obtained by fly-boys are not representative of the population structure. Page (7) shows that in his samples rates of infections in *fusca* group and game tsetse are much higher than those for *G. palpalis* and that female flies seem to be more dangerous.

Traps catch a larger number of species, a higher ratio of animal trypanosomiasis vector

TABLE 1
Records of tsetse in various localities

Locality	Survey old — pre 1951 new—1951-1955	*G. palpalis*	*G. tachinoides*	*G. pallicera*	*G. fusca*	*G. nigrofusca*	*G. tabaniformis*	*G. medicorum*	*G. longipalpis*	*G. morsitans*	Remarks
Kintampo	old	+			+				+		3 sp.
8°3′N & 1°42′W	new	+		+		+			+		4 sp. 2 new
Bericum	old	+							+ ?		2 sp. ? mapping
7°28′N & 2°35′W	new	+		+		+					3 sp. 2 new
Ejura	old	+		+	+				+		4 sp.
7°19′N & 1°22′W	new	+		+	+	+	+		+		6 sp. 2 new
Mampong	old	+				+					2 sp.
7°4′N & 1°25′W	new	+		+		+					3 sp. 1 new
Prasu	old	+		+							2 sp.
5°56′N & 1°26′W	new	+		+	+	+					4 sp. 2 new
Foso	old	+									1 sp.
5°42′N & 1°16′W	new	+				+					2 sp. 1 new
Asuansi	old	+							+ ?		2 sp. ? mapping
5°16′N & 1°15′W	new	+				+					2 sp. 1 new
Ankaful	old	+			+ ?				+		3 sp. ? identif.
5°7′N & 1°19′W	new	+				+	+	+	+		5 sp. 3 new
Elmina	old	+			+ ?				+		3 sp. ? identif.
5°5′N & 1°21′W	new	+						+	+		3 sp. 1 new
Pokoase	old	+							+		2 sp.
5°40′N & 0°15′W	new	+						+	+		3 sp. 1 new
Southern Savannah	old	?									? suspected
about 6°N & 0°30′E	new	+									1 sp. 1 new
Kpeve	old	+							+ ?		2 sp. ? mapping
6°40′N & 0°22′E	new	+			+						2 sp. 1 new
Akroso	old	+	+						+	+	4 sp.
7°25′N & 0°12′E	new	+	+		+				+		4 sp. 1 new
Kpechu	old	+	+		+				+	+	5 sp.
7°50′N & 0°3′E	new	+	+					+	+		4 sp. 1 new

TABLE 2
Tsetse records for 2 localities

Locality and area and duration	Method of survey	No. captured	Species ratio in %			♀%		
		All species of *Glossina*	*G. palpalis*	*G. pallicera*	*G. nigrofusca*	*G. palpalis*	*G. pallicera*	*G. nigrofusca*
Wiwi River (Kumasi) 17 months	Fly-round	1652	99·3	0·4	0·3	53	—	—
	Traps	1355	88·5	5·4	6·1	68	47	34
Berikum 2 months	Fly-round	243	99·2	0·8	0	47	—	—
	Traps	284	76·1	2·1	21·8	64	—	53

flies, a higher proportion of females, and older flies i.e. provide more information important in consideration of epidemiology of animal trypanosomiasis.

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ETUDE DE CARACTERES MORPHOLOGIQUES ET ANATOMIQUES EN RELATION AVEC L'AGE PHYSIOLOGIQUES DES FEMELLES DE GLOSSINES

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A Brazzaville, une étude des caractères morphologiques et anatomiques en relation avec l'âge physiologique des femelles de glossines a été faite sur *Glossina palpalis palpalis* (Rob.-Desv.) et *Gl. fuscipes quanzensis* Pires. Ces femelles avaient été récoltées dans la nature puis mises en élevage.

Sur chaque glossine, il a été procédé aux observations suivantes:

(1) Présence ou absence de marques ou cicatrices externes de copulation ou mating scars: caractère déjà étudié par Squire (1960-62);

(2) Après dissection de l'appareil génital dans de l'eau physiologique:
—présence ou absence de spermatozoïdes dans les spermathèques,
—nombre de dilatations avec relique folliculaire sur le funicule de chaque ovariole,
—présence ou absence d'oeuf ou de larve dans l'utérus,
—nombre de cellules nourricières de l'oeuf.

Ces observations ont été faites sur plus de 1000 glossines.

Tous les âges physiologiques, depuis la femelle nullipare jusqu'à la femelle ayant donné six pupes ont été observés et décrits. S'y ajoute quelques cas anormaux: femelle n'ayant qu'un ovaire fonctionnel, femelle présentant un ovariole bloqué avec un oeuf résiduel dégénéré. Une vingtaine de planches que l'auteur commente illustrent ces observations.

Le nombre de cellules nourricières de l'oeuf a pu être évalué. Dans de nombreux cas et en utilisant deux techniques différentes l'auteur en a compté 15 chez les deux espèces précitées. Saunders (1960) chez *Gl. morsitans* en avait compté 14. Ces 15 cellules sont de taille diffférente, il a été possible d'observer:
—un groupe de 4 cellules plus grosses que les autres,
—un groupe de 6 cellules moyennes,
—un groupe de 5 cellules plus petites.

Plus de 24 cellules nourricières ont été comptées, une fois, chez une femelle de *Gl. fuscipes quanzensis.*

Sur chaque femelle, l'étude du tractus génital et des marques externes de copulation a permis les conclusions suivantes:
—il semble exclu chez ces deux espèces des environs de Brazzaville, de pouvoir prendre comme critère de non fécondation, l'absence de marques externes de copulation, vu que sur 466 *Gl. fuscipes quanzensis* et 169 *Gl. palpalis palpalis* fécondées, 48·9% des premières et 38·5% des secondes ne portaient aucune marque.
—il a été constaté que le pourcentage des femelles présentant ces cicatrices augmente avec l'âge physiologique.
—il arrive fréquemment aussi que de vieilles mouches portent des marques très légères et que de jeunes mouches présentent de très larges cicatrices.

(Cette étude est en cours de publication dans les "Cahiers O.R.S.T.O.M., n°2, Paris, 1964).

RESEARCH ON *MUSCA AUTUMNALIS* DEG. IN THE UNITED STATES

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Musca autumnalis DeGeer has become one of the most important dipterous pests of cattle and horses in eastern United States. The development of a satisfactory rearing procedure has facilitated biological and control studies. Average duration of life stages at 27°C. is as follows: egg—16 hours, larval—4 days, and pupal—7 to 8 days. Data from laboratory reared and field collected strains are very similar.

When reared adults were held at 27°C., mating was observed at 2 to 11 days of age. First eggs were produced 96 hours after eclosion. Eggs were produced at a maximum age of 48 days. 80% of the eggs were laid in the first 3 weeks of adult life, with approximately equal numbers being produced per week. Maximum longevity of adults was 55 days. Seventy-one flies of unknown sex ratio produced 5,050 F_1 pupae.

Pupae are able to withstand humidities ranging from 40% to 93% at 25°C., as there was complete adult emergence at both extremes tested.

Although photoperiod likely plays a part in causing the flies to hibernate, this has not been investigated in any detail. Newly emerged flies exposed to 10 hour day of 3,500 foot-candle intensity, with daytime temperature of 27°C. and night temperature of 20°C., laid eggs normally.

Changes in bovine diet are reflected by variation in the attractiveness of the resulting feces for oviposition by *M. autumnalis*. Although it is suspected that there may be a correlation of attractiveness for oviposition with moisture content of feces, this can not be demonstrated with presently available data.

Aphaereta pallipes (Say) and *Eucoila* sp. have been observed to parasitize *M. autumnalis* in Ohio. Of 2,025 third instar larvae and pupae collected in 1963, 1·04% were parasitized by the cynipid and 2·37% by the braconid. A maximum of 52% of the larvae in individual dung piles was observed to be parasitized by the cynipid and 21% by the braconid. Thirty three per cent of dung piles examined contained parasitized larvae. When parasitized larvae were brought into the laboratory and held through the pupal stage, the parasites were never able to emerge through the host puparium.

Certain habits of *M. autumnalis* have made it difficult to control. These include: (1) only a small portion of the flies are on the animals at any time; (2) the flies feed around the eyes and muzzle, in locations where it is difficult to maintain effective insecticidal residues; and (3) there is considerable movement of flies from animal to animal, and among herds.

Various sprays, dusts, and smears have been tested in an attempt to find a suitable control measure. Daily application of Ciodrin (*a*-methylbenzyl 3-(dimethoxyphosphinyloxy)-*cis*-crotonate) or dichlorvos (*O*, *O*-dimethyl 2,2-dichlorovinyl phosphate) in corn sirup has given best results, but is laborious and therefore inappropriate for beef cattle.

The addition of a larvicide to the bovine diet will prevent *M. autumnalis* breeding in the resulting feces, but will not alleviate the fly problem because of continued movement of flies into the treatment area.

SYNANTHROPY OF BLOWFLIES

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The distribution of many animals shows a clear dependence on conditions created by man. This biocoenotic dependence is known as synanthropy. Its mode and degree differ in different species. The degree of synanthropy of a given species shows considerable regional variations. An exact knowledge of the reasons which have given noxious synthropes their ability to live in conditions created by man must be the basis for their rational eradication. Comparable evidence about the degree of synanthropy from different parts of the world would thus be desirable.

To obtain comparable data on the degree of synanthropy of blowflies I have adopted a definite investigation procedure and an index to express the degree of synanthropy (3). To obtain material for the calculation of the synanthropic index, it is necessary to perform comparable trappings simultaneously in a city, at an isolated rural house and in the wild. To calculate the index from the material obtained the following formula is used:

$$\frac{2a+b-2c}{2}$$

In this formula, a is the percentage of specimens of a given fly species trapped in a city relative to all specimens of this species trapped at the three observation stations. b is the respective percentage of specimens trapped at the isolated rural house and c the percentage of specimens trapped in the wild. The synanthropic index ranges between $+100$ and -100, the former representing the highest degree of synanthropy. Negative values indicate avoidance of man.

Trappings performed in such a way that calculation of the synanthropic index has been possible have been made in Hungary (2), Czechoslovakia (1) and Sweden (4), and in three vegetational zones of Finland (3). These investigations reveal the existence of considerable regional differences in the degree of synanthropy. Generally the synanthropy increases towards the borders of the ranges.

The ecology of flies in their original biotopes provides a key for understanding their ability to live in natural conditions. Of the three blowflies showing a high degree of synanthropy in Central- or South-Finland, two (*Phormia terrae-novae* R.-D. and *Calliphora uralensis* Vill.) have their natural biotopes in the subarctic or arctic (3, 6-8). Their high ecological valence, which has developed as an adaptation to arctic conditions, seems to make their life possible in city conditions too. Rapid larval development is especially important in city conditions where garbage collection inhibits delayed development. The archipelago of southern Finland, with its thousands of small isolated rock islets, seems to form a city-like environment suitable for the synanthropic species *Calliphora uralensis* and *Lucilia sericata* (Meig.) in an area generally unsuitable for them.

The importance of studies on the synanthropy problem increases simultaneously with the exponentially increasing human population. Synanthropy is an international problem needing standardized study methods. The author hopes that the experimental procedure and index described may be adopted as standard methods.

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QUANTITATION OF EXPERIMENTAL TRANSMISSION OF *SALMONELLA TYPHIMURIUM* BY HOUSEFLIES TO MAN

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Surprisingly neglected in previous studies of flies and disease is whether contaminated flies can transmit sufficient organisms to produce infection in animals and man. This paper describes an experimental cycle, quantitating the transmission of *Salmonella typhimurium* from the feces of an infected dog to houseflies, thence to food and human volunteers. Use of a streptomycin-resistant strain of *S. typhimurium* and incorporation of 2,000 λ dihydrostreptomycin per ml. of SS or EMB agar permitted direct enumeration of the pathogen while all other organisms were suppressed. Its IP mouse virulence was equal to that of a strain freshly isolated from a patient in Mexico City.

A pathogen-free dog drank 210×10^8 *S. typhimurium* in milk. Its feces, 26 hours later, were quantitated and samples were exposed for two hours in fly cages which housed 3 adult *Musca domestica* per cage. The following morning, the flies were allowed to feed on atole, a popular Mexican drink, which after a $10\frac{1}{2}$-hour standing period at 30°C was sampled and then ingested by volunteers. Volunteers were selected on the basis that they were free of enteropathogenic bacteria and GI symptoms, and had no significant agglutinin titers for *S. typhimurium* and related organisms.

Twenty hours after fecal exposure, the flies were quantitatively and qualitatively processed. Despite their uniform age, nutrition and previous microbial exposure, fly contamination with *S. typhimurium* was sporadic, even among cage-mates. Degree of contamination ranged from 43 to 635 organisms per fly. Five of 20 flies (25%) quantitatively tested were positive, whereas 6 of 15 flies (40%) passed through tetrathionate enrichment were positive (including 5 flies from auxiliary cages). The dog's feces contained an average of 10^5 *S. typhimurium*/gm which is 4 logs lower than the number of pathogenic *Escherichia coli* known to be excreted in clinical cases, and 2 logs lower than excretion rates in shigellosis and salmonellosis. This probably contributed to lower fly counts. Actual levels in the flies were at least 100 times below the 10^4 level suggested by others as the minimum necessary for multiplication of *Salmonella* and other pathogens.

Flies succeeded in contaminating 8 of the 10 atole specimens, which after the $10\frac{1}{2}$-hour standing period contained 5×10^3 to 64×10^4 *S. typhimurium*. It was verified that a prolongation of the fly-atole exposure period and/or the atole standing period to 24 hours (its palatability remaining unchanged) would have produced a significant human infective dose.

S. typhimurium was recovered from the feces of 6 of the 10 volunteers, once per volunteer, during a 15-day sampling period. Earliest recovery was 15 hours and the latest, 4 days. Passage of the pathogen through the GI tract was asymptomatic and evoked no antibody response during the 3-week observation period. Absence of symptomatology was not due to lack of virulence but to the subthreshold dose of 10^5, about 100 times lower than the number needed to produce symptomatic salmonellosis in adults. The same dose or even less may, however, suffice to produce illness in children.

Comparison of the quantitative aspects of fly-poliovirus transmission suggests that the lower titer of virus in stools may be offset by lower infection thresholds in fly and man. Flies must be able to deliver an infectious dose since virus does not multiply in food.

Direct fly transmission of enteric infection to human adults appears doubtful where generally high infective doses are required. It seems likely, on the basis of this preliminary study ,that bacterial infections can be potentiated by fly contamination of food.

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THE DISTRIBUTIONAL PATTERN OF *LIPOPTENA CERVI* ON DANISH RED DEER (*CERVUS ELAPHUS* (L.)) AND FALLOW DEER (*DAMA DAMA* (L.)).

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From September to December 1960, 87 female and 94 male deer keds (*Lipoptena cervi*) were combed out of the coat of red deer (6♀♀, 6♂♂) and fallow deer (6♀♀, 5♂♂, 11 juv.) from Jaegersborg Deerpark, north of Copenhagen. The deer had been recently shot. On the fallow deer only one ked was found, while on the red deer the frequency of infestation was 92% with a density range of 0-63 keds (average about 15) per red deer.

More than 90% on the red deer were collected from neck (25%)—groin (23%)—flank (20%)—anal region (16%)—axilla (12%), while on head (3%)—belly (2%)—back (0%) only a few specimens were found. The flank is omitted in the following because it is regarded as an intermediate region between neighbouring niches, also the head as this microhabitat might deserve further subdivisions (ear, nostrils etc.), which however was impossible to do on account of the few keds available.

It was decided to study the ecological features of the following niches: back, neck, axilla, belly, groin, anal region, and their bearing on the distributional pattern of deer keds on the red deer.

(1) Although the ectoparasites may tend to aggregate, the small number of species and on healthy deer of specimens, makes it highly improbable that there should be any negative interrelationship indicating competition for space and food between the ectoparasitic individuals including deer keds on red deer.

(2) Persecution from the host will certainly occur whenever possible and of course especially where the niches are within easy reach for mouth and hoofs of the host. Back, neck, anal region and perhaps axilla may then be the safest areas for the keds.

(3) Persecution from other animals than the host will be negligible.

(4) Skin and rectal temperature were measured on 4 red deer (148 records) immediately after they were shot, and the following average values found: rectum, 39°C—back, 34°C—neck, 35°C—axilla, 37°C—belly, 34°C—groin, 37°C—anal region, 33°C. On the basis of temperature distribution alone it seems however difficult to explain the relative distribution of deer keds. Other factors must be included.

(5) Humidity in coat was disregarded because the keds will get a surplus of water through their food.

(6) On 3 red deer, microstructure of skin and dimensions and relative numbers of hairs from the microhabitats were studied. Preliminary studies on mouthparts and claws had shown the keds to be pool feeders and best adapted for attachment to wool or to contour hairs with diameters maximally like those in axilla and groin. Easiest access to blood vessels, least number of elastic fibres in corium, and presence of relatively many small-dimensioned hairs made neck, axilla, and groin most favourable to the deer keds.

The conclusion of this analysis is that no single factor can be singled out as a key factor in determining the distributional pattern of the deer keds. In each niche the ked population will naturally depend on a balance of several more or less important factors. Thus it would seem that the surface of a healthy red deer offers two centres of distribution: one around axilla-neck, the other around the groin-anal region.

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PHYSIOLOGY AND BIOCHEMISTRY OF BLOOD-SUCKING INSECTS

ANALYSIS OF THE OVERALL LAYING-CYCLE IN A POPULATION OF INSECTS

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It is well known that mosquitoes exhibit alternating periods of activity and rest, and that the periods of activity each day may occupy only a small proportion of each 24 hours. While activity-cycles can be observed and recorded in great detail in the field, it is difficult to do anything but speculate on the underlying factors responsible, as one has no control over the environment. Recently, however, cyclic activity has been studied in the laboratory in collaboration with Dr. A. J. Haddow and Dr. P. S. Corbet, and the overall oviposition cycle of *A. aegypti* has been studied in considerable detail.

In a population of this species reared and kept under conditions of alternating 12 hours light and 12 hours dark, a wave of egg-laying activity occurs at the same time each day, eggs being laid during a clear-out *laying-period* just before sundown each day. The same thing occurs even when artificial lights are used and the changes from light to dark and from dark to light are abrupt, the laying-period occurring just before the lights are turned off. The cycle continues to bear the same relation to light and dark even when these are artificially reversed or are reduced or extended within wide limits. Cyclic activity is still shown with only 5 minutes light per day.

Under conditions of continuous light or continuous dark no such rhythm occurs. A single exposure to light, however, in an otherwise all dark existence is enough to change acyclic to cyclic behaviour, the first oviposition peak appearing 20-24 hours after the return to darkness, irrespective of the duration of exposure to light; a single exposure of only 5 sec. duration is enough to allow the return to darkness to be effective as a time-cue.

A single change from conditions of continuous light to those of continuous dark is also followed by a change from acyclic to cyclic behaviour, the first peak of activity appearing 20-24 hours after the onset of darkness, with subsequent peaks at successive 24 hour intervals. No cyclic behaviour follows the reciprocal change. It is clear, therefore, that, although the rhythm is largely endogenous, onset of darkness is the time-cue on which overt cyclic behaviour is based.

Similar findings have been demonstrated in preliminary experiments on the sugar-feeding cycle in this species, but there are morning and evening peaks of activity each day. Double peaking in sugar-feeding cycles has been recorded in the field by several observers.

Within wide limits the oviposition-rhythm is independent of temperature, although ovarian development itself is known to be temperature dependent. At 29°C the interval between taking a blood meal and the completion of ovarian development in *A. aegypti* is about 40 hours and the regular 24-hour cycle in a population must obviously be a statistical effect dependent on numbers. Only if all the female mosquitoes took their first blood meal simultaneously, and laid all their eggs at a single sitting, could there be 100 per cent representation. In this event, however, the shortest interval between peaks would be 48 hours. By dividing small populations of this species into pairs (male and female), and by giving each pair continuous opportunities for fruit-feeding, mating, blood-feeding and egg-laying, it has now been possible to analyse the oviposition-cycle in terms of the contributions made by individual members of the population, precaution being taken to ensure that the mosquitoes emerged over a period of about 36 hours so as to avoid any tendency towards simultaneous feeding.

Under conditions of alternating 12 hours light and 12 hours dark each mosquito that has completed ovarian development following a blood meal withholds its eggs until the arrival of the first "available" laying-period, that is, until the first 20-24 hours period following the last change from light to dark. Thus, except when completion of ovarian development coincides with the arrival of a laying-period, synchrony of laying in a population is achieved by delay,

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for obviously the eggs cannot be laid before they are mature. Delay in laying by a proportion of the insects and the out-of-phase feeding normally expected in a population of heterogeneous age, is enough to ensure that contributions to the oviposition-cycle are made by some of the mosquitoes each day.

Each mosquito does not always lay all her eggs during the first laying-period following completion of ovarian development, but may retain some or even all of them for a further 24 hours. Indeed, egg-laying, once started, may go on in discrete 24-hourly instalments for two or three days before the next blood meal is taken. It seems that there is a rhythmic laying urge of limited duration every 24 hours, and that if for some reason all the eggs are not laid during the first laying-period, the remaining eggs are retained until the next.

Under conditions of continuous light each mosquito tends to start laying its eggs independently as soon as ovarian development is complete, but egg-laying may then continue for 12 hours or more. This results in the typical acyclic laying characteristic of a population kept in continuous light. When, however, continuous light is changed to continuous dark, asynchronous laying is replaced by synchronous laying. Any mosquito that has completed ovarian development at or soon after the change from light to dark delays egg-laying until 24 hours after the change; any mosquito that has not by then completed ovarian development delays egg-laying for a further 24 hours, that is until 48 hours after the single change from light to dark. At lower temperatures she will presumably delay until 72 or 96 hours after the change.

From this work it is seen that irrespective of the time of completion of ovarian development, each mosquito normally delays oviposition until just before "sunset", even when the change from light to dark, is abrupt. The time-cue provided by the change from light to dark acting through the basic 24 hour rhythm of the insect, serves as a synchronizer which ensures that eggs are laid just before sunset, even when photo-period is lengthened or shortened within wide limits. Thus, no matter how day-length changes with season, egg-laying will occur just before sunset. Is this period of the day particularly favourable for egg-laying or egg-survival, or is it the optimum time for flight activity in general for this species, for flight activity must precede actual egg-laying?

LIGHT INTENSITY AND ENDOGENOUS RHYTHM IN RELATION TO CREPUSCULAR BITING ACTIVITY IN FOREST MOSQUITOES

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Many mosquitoes of the tropical forest show marked surges of biting activity in the hour after sunset and that before sunrise. The sunset peak is almost invariably the larger. With increasing height above ground these peaks become progressively more accentuated till above the canopy they may represent almost the total biting activity.

Work carried out above the forest canopy, at 80 feet, on a high steel tower nine miles from the equator, has permitted study of such crepuscular behaviour in relation to zenith light without interference from foliage. Biting peaks are very pronounced at this height. The zone is important as thermal convection currents, forming over tropical forest after sunset may disperse small insects widely, and it is known that virus-infected mosquitoes occur above the canopy at this crucial time.

For crepuscular work E. T. Nielsen suggests as a unit the crep, or duration of civil twilight. At the equator, however, where twilight is of virtually constant duration, with crep 1 about 22 minutes after sunset, actual time units may be used (ten-minute periods in the present work). Sunset is here by definition 18 hours, sunrise 06 hours.

In the evening twilight many species rise from the forest floor to the canopy or to levels above it. The reverse occurs in the morning. This takes some time and evening biting-peaks occur progressively later with increasing height, the reverse again applying in the morning. Light is the only environmental factor changing with sufficient rapidity to explain these surges of biting activity and it was believed that mosquitoes followed up a light-gradient,

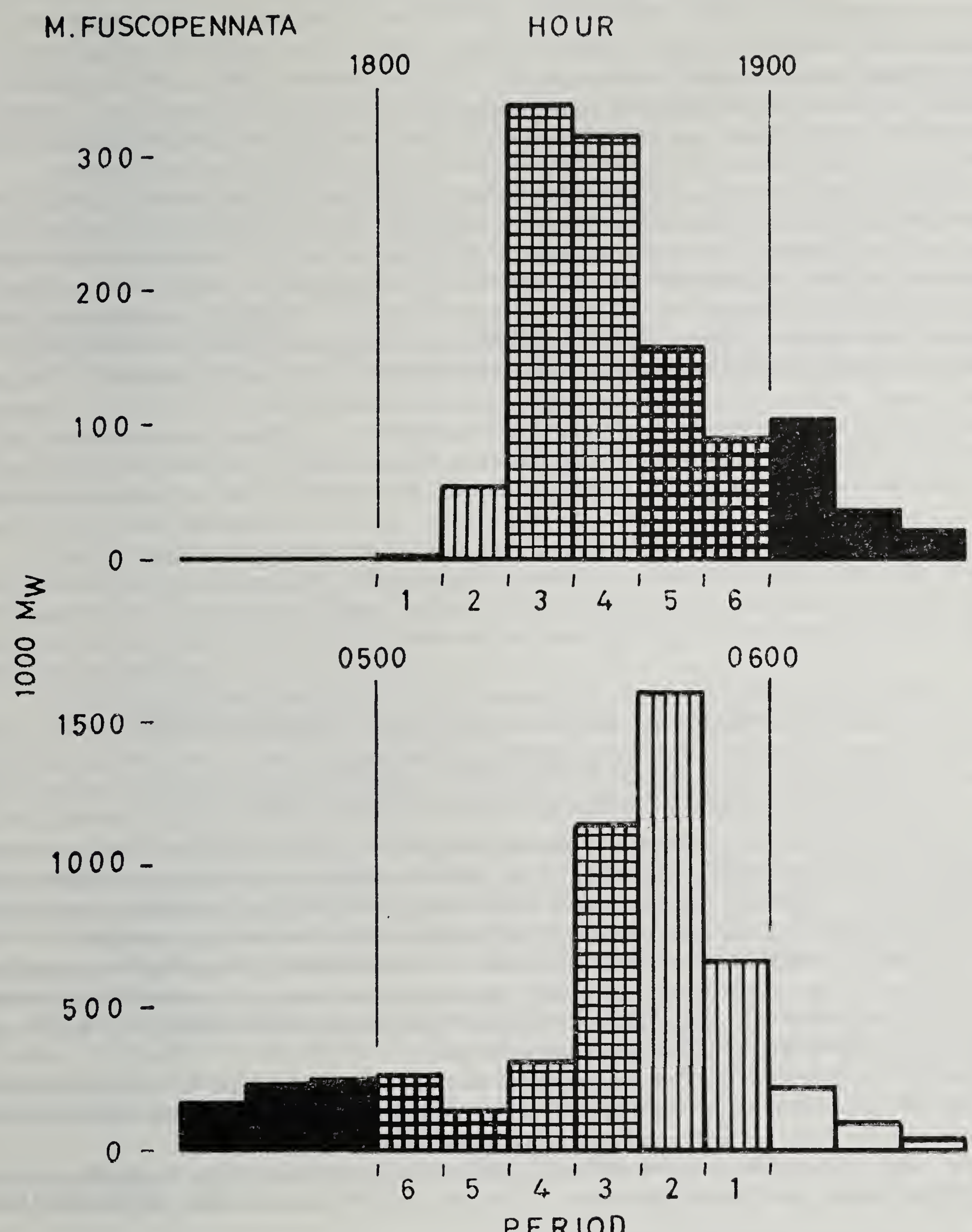

Fig. 1. The biting-activity of *Mansonia fuscopennata* by 10-minute periods, around sunset (1800 hours, above) and sunrise (0600 hours, below) above the forest canopy (Williams' mean). The scales have been adjusted so that the greatest height of each histogram is the same. Shading roughly indicates degree of darkness. Periods 1 and 2 approximate to crep 0-1, periods 3 and 4 to crep 1-2 and periods 5 and 6 to crep 2-3.

reaching maximum activity at each successive level as light attained some particular value or rate of change.

If this were so, evening peaks should occur in the same relation to sunset as morning peaks to sunrise. It has been found, however, that in the seven species studied which exhibit biphasic crepuscular behaviour the morning peak is closer to sunrise than the evening one is to sunset, the shift usually being one 10-minute period. This seems a small difference, but at the equator light changes so rapidly during twilight than the 10-minute shift in *Mansonia fuscopennata* (fig. 1) means that the morning peak reaches its height at a light intensity 13 times as great as that in the evening. *Aedes ingrami* is an extreme example, the morning peak reaching its height at a light intensity 150 times that obtaining at the height of the evening peak.

Almost certainly a strong endogenous component triggered by light dominates the evening activity peaks. The morning peaks, however, occur not 12 but 11 hours later and, as now shown, under different light conditions, nor do differences in spectral composition at sunset and sunrise explain the phenomenon adequately. Usually evening and morning peaks do begin at similar light intensities, but while one continues into gathering darkness, the other continues into growing light. Neither endogenous 24-hour rhythm nor environmental influence adequately explain this obscure phenomenon which is still under intensive study.

HOST FINDING REACTIONS OF SOME SIPHONAPTERA

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One of the most critical moments in the life history of the flea occurs when it emerges from pupation. Within a relatively short time, it must find a suitable host and secure a blood meal, or it will perish. Later the flea may leave and return to the host, and each time it must find a suitable host, although the time element is not so critical after the flea has once fed.

It is evident, therefore, that adult fleas must have some means of locating and orienting toward a host. One might suspect that they also have some means of recognizing a suitable host, that is one which will permit them to complete their life cycle successfully. It is with the first of these phenomena that this paper is concerned.

Several workers have studied this problem, and have presented data to indicate that the stimulus for host-finding is (*a*) temperature, or warmth of the host; (*b*) air currents caused by movement of the host; (*c*) CO_2 produced by respiration of the host.

We have studied four species of fleas as follows: *Ctenocephalides felis*, *Oropsylla arctomys*, *Ceratophyllus riparius*, and *Ceratophyllus idius*. The first two are mammal fleas, the last two bird fleas.

C. felis showed marked positive reactions to temperature and carbon dioxide. In an olfactometer, it reacted positively to the presence of a host, but whether this was due to host odor or carbon dioxide was not determined.

O. arctomys did not respond positively to any of the stimuli presented, and failed to react positively in olfactometer tests.

C. riparius and *C. idius* responded only to air movement. Their response to this stimulus did not appear to be directed. Apparently air movement such as might be caused by a bird's wings causes them to leap in a more or less random manner.

We conclude that each species has its own method of host-finding, and that no generalization can be made as to the method of host-finding until a given species has been tested.

STRUCTURE AND FUNCTION OF THE GUSTATORY ORGANS OF THE MOSQUITO

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This report is based on an investigation of contact chemoreception in the mosquito *Culiseta inornata* (Williston). Attention has been given to the identity and morphology of the chemoreceptor organs, thresholds of acceptance, responses mediated by different groups of taste receptors, the function of each receptor group in feeding, and the hierarchy of command among the taste receptors over feeding.

The data presented are taken in part from Feir, Lengy, and Owen (1) and Owen (2). Sensitivity of the taste receptors on the tarsi and labella was tested by determining acceptance thresholds for sugars. The results clearly show that the mosquito can distinguish degrees of sweetness. The order of stimulative effectiveness for the following sugars was: sucrose > maltose > fructose > glucose.

Chemosensory hairs bearing taste receptors have been identified on the tarsi, labella and ligula. Stimulating these sensilla with water and acceptable solutions elicits characteristic responses. The tarsal and labellar hairs arise from sockets, have two cavities, and taper to blunt tips with minute papillae. At the base of a labellar hair are three or four bipolar neurons. The distal fiber from one of these neurons terminates at the base of the hair, while this fiber of the others enters the thick-walled cavity (Zwonitzer, 1962). A ligular hair has only one cavity and tapers to a sharp point.

Observations on mosquitoes with their stylets unsheathed suggested the presence of taste receptors within the cibarium. Experimental evidence in support of this view was obtained by piercing the clypeus and dorsal surface of the cibarium and introducing a 1M sucrose solution with a micropipette. The presence of sugar in the cibarium elicited the labellar response immediately.

Under appropriate conditions all the chemosensory hairs identified will mediate sucking. Stimulating the labellar and ligular hairs with water and sugars elicited feeding responses, but blood was ineffective. Receptors within the cibarium are sensitive to water, sugars and blood. The stylets do not have taste receptors. All the evidence indicates that gustatory organs on the proboscis play no part in sucking blood. Blood drawn into the cibarium stimulates receptors to provide the sensory input for maintaining sucking. The factors which induce host-seeking and biting also evoke sucking during probing. This has been confirmed by observing a mosquito at 60 magnifications while she was in the act of probing. From these and other observations it was concluded that, with the exception of the cibarial receptors, the sensory mechanisms used in probing and sucking blood differ from those employed in feeding on carbohydrates.

Taste receptors within the cibarium exercise ultimate control over the imbibition of fluids. In like manner, the labellar and ligular receptors dominate those on the tarsi. Recent experimental evidence supports the view that the hierarchy of command over feeding, other than sucking blood, in ascending order is: tarsi, labella = ligula, receptors in the cibarium.

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A COMPARISON OF OESTROGENS AND AMINO ACIDS AS ATTRACTANTS FOR *AEDES AEGYPTI* MOSQUITOES

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Certain oestrogens having proved attractive to female *Aedes aegypti* in olfactometer tests, and lysine and some other amino-acids having proved attractive in a free-flight cage, studies were undertaken on both these groups of compounds utilizing both types of test method.

Lysine, whose attractiveness is in direct ratio to its content of both adsorbed carbon dioxide and of CO_2 in carbaminoyl or other loose type of combination, proved to be attractive in the olfactometer in amounts ranging from 10^{-2} down to 10^{-8} gm., corresponding to concentrations down to 0·01 p.p.m., as compared to the threshold of 1 p.p.m. formerly found for its activity in the free-flight cage.

Oestriol when tested in the free-flight cage showed attractiveness only in the initial test performed each day, while the tests performed immediately following gave approach ratios indicating repellency. However, it was observed that the first time oestriol was exposed each day, it was attractive. Therefore the free-flight cage was isolated from extraneous influences by being enclosed in glass, and the accumulation of vapours inside was prevented by providing an airstream across the exposure dishes and exhausted from the top of the cage. Under these conditions oestriol proved to be attractive at virtually all concentrations from 10^{-6} down to 10^{-16} gm. of the material exposed, similar to the results previously obtained in the olfactometer. It is evident that whereas lysine shows the higher attractiveness, oestriol remains attractive at much lower concentrations.

When 26 L α-amino acids were tested in the open free-flight cage, significant attractiveness was found for lysine, arginine, tyrosine, threonine, alanine, glutamine and l-methylhistidine. These amino acids were retested in the glass-enclosed free-flight cage, having been also chemically assessed in aqueous solution for their carbaminoyl and free CO_2 content, by means of barium hydroxide. The basic amino acids lysine, arginine, histidine and their l-methyl and 3-methyl derivatives proved considerably attractive, and contained both carbaminoyl and adsorbed CO_2. Threonine, alanine and glutamine, and in addition asparagine and serine, were significantly attractive; these contained small amounts of adsorbed CO_2 only. Tyrosine, and in addition proline, hydroxyproline and cystine were significantly attractive without containing any CO_2 at all in their solutions. The other amino acids showed no attraction, and some of them a slight repellency.

When the attractiveness of human arms to *Aedes aegypti* was assessed in terms of alighting values, it was found greater in females than in males and to show cyclic changes during the menstrual cycle. It showed 4 peaks of attractiveness, the first at day 13 at the time of ovulation, then 2 peaks between days 18 and 23 during the corpus luteum activity, and the last 1 day before the end of the cycle. From what is known of urinary excretion during the menstrual cycle, the first 3 peaks correspond with maxima of oestrogen production, and the 4th with maximum production of ketosteroids.

Traps providing warmth, moisture and CO_2 were made more effective than animal- or bird-baited traps to *Aedes* mosquitoes in southern Germany when lysine or tyrosine was added. The substitution of oestriol was even more effective, but the addition of oestriol to the amino-acid was the most effective.

It is concluded that both the oestrogens produced in smaller amounts by the human body, and amino acids such as lysine produced in larger amounts, are of approximately equal importance in increasing the number of *Aedes* mosquitoes brought by visual factors, warmth and humidity to the human host.

ATTRACTIONS OF SOME SIMULIIDS TO ETHER EXTRACTS FROM BIRDS AND TO CARBON DIOXIDE

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Discovery of the specific feeding behaviour of some ornithophilic simuliids (1, 2) and the significant observations of Lowther and Wood (4) led to the present observations on the attraction of black flies to various olfactory stimuli. Preliminary results (3) support the view that some simuliids are attracted to specific olfactory stimuli and others to CO_2 alone.

A dead loon (*Gavia immer*) kept at 0°F was removed from the freezer and placed immediately on the shore of Lake Sasajewan in May. Within two minutes scores of flies hovered about and landed on the feathers of the frozen bird. They were so abundant a sample of ten flies was easily aspirated from the air; all were *Simulium euryadminiculum.* Samples of the flies attracted to the dead bird were obtained by sweeps with an insect net over the dead bird and by dropping a $2 \times 2 \times 2$ foot fine mesh cage over it and collecting the trapped flies. Both methods confirmed the unmistakable qualitative observations that *S. euryadminiculum* was attracted to the dead loon. Flies landed on the dark feathers on the head, neck, and back of the loon but not on the white feathers on the underside. Flies that landed on the head and neck crawled among the feathers. Flies hovered also over a dark object placed on the board on which the loon had been lying and around a nearby log projecting from the lake. This suggested that attraction might result from visual rather than olfactory stimuli. However, flies approached a mesh cage in which the loon was enclosed and also the carcass of the bird from which the skin was removed.

Portions of the carcass of the loon were placed in acetone, ether, and a detergent, and samples of the liquids were poured slowly on filter papers. The papers, thus saturated with the extracts, were then placed four feet apart along the lake shore. Almost immediately flies hovered over the papers saturated with acetone and ether extracts prepared from the tail of the loon. Some flies landed momentarily on the papers raised in a "hump" but not when they were flat on the ground. Extracts from loons have been fractionated by Dr. A. Shaw of the Department of Chemistry using gas and thin-layer chromatography to try to isolate and identify components that attract the flies.

These observations support the hypothesis that *S. euryadminiculum* is attracted to the common loon by odours but landing may be determined by visual stimuli and touch determines whether the flies crawl among the feathers.

Attention was directed next to *Simulium rugglesi* that feeds commonly on ducks. Numerous specimens were attracted to dead ducks when CO_2 was released beside them. Similarly the ether extract of the uropygial glands of ducks attracted *S. rugglesi* only when CO_2 (ca 30 ml/min.) was emitted simultaneously. Many flies were attracted to the CO_2 alone but more to the CO_2 plus extract. Samples of flies were captured by placing the stimuli at the open bottom of a fine mesh white cage suspended 8 inches above the ground at the lake shore. Few flies were captured when the cage was suspended 10 feet above the ground.

Simulium aureum, S. latipes, S. quebecense, S. croxtoni and *Prosimulium decemarticulatum*, that feed on birds in the forest canopy, were attracted to CO_2 alone when it was released (ca 30 ml/min.) beneath $2 \times 2 \times 2$ foot cages suspended 10-15 feet above the ground in the forest.

These observations suggest that females of several simuliids are attracted to olfactory stimuli some of which are specific and others are common to several animals. Visual stimuli may be more important in attracting some species than others and touch may partially determine the site on which the flies feed. Attraction of different flies to suitable olfactory and visual stimuli will occur if they are provided in the habitats favoured by the species of fly.

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THE EFFECT OF CHEMICAL STIMULI ON SOME FEEDING RESPONSES OF THE STABLE FLY (*STOMOXYS CALCITRANS* (L.))

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Four feeding responses which *Stomoxys* may make on a mammalian host are (*a*) extension of the proboscis (*b*) probing (this is a vigorous thrusting movement of the extended proboscis and may be repeated many times), (*c*) biting (a cutting action of the labellar teeth during which the extended proboscis remains relatively motionless), and (*d*) ingestion.

Neither probing nor biting are obligatory responses in the feeding pattern as *Stomoxys* will readily imbibe withdrawn blood.

Only a very preliminary study was made of the biting response to several contact and vapour stimuli using the number of holes bitten through filter paper as a measure of response (2). Blood as a contact stimulus was very effective in stimulating biting and the stimulating property resided entirely in the corpuscle fraction. Neither blood vapour nor ammonia vapour were stimulating although the latter is a strong probing stimulant. Sucrose solution was ineffective as a biting stimulus although it induced proboscis extension. Heat did not appear to contribute any stimulating effect. Normally the surface of the host's skin provides the biting stimulus and it is possible that blood cells and skin cells possess common stimulating properties.

Probing is induced by a group of stimuli which are token indicators of the presence of blood, such as mammalian skin odours (1) and pure vapours such as ammonia which are components of skin odour. The function of probing is to stimulate a searching movement with the extended proboscis thus increasing the chances of encountering contact stimuli which will induce biting. The vapour above 1 ml. of 0·16% ammonia solution (approximately 1·1 mgms ammonia per litre air) stimulated probing in nearly 60% of 2-6 day old flies 24 hours after satiation on blood. Saturated water vapour also possessed some stimulating effect. Feeding to satiation on either withdrawn pigs blood or on 0·5 M sucrose solution (the former is taken into the midgut, the latter into the crop) caused an immediate rise in probing threshold. Lower, but still readily acceptable sucrose concentrations (e.g. 0·18M) although imbibed in larger volume than 2·0 M sucrose solution did not appreciably effect the probing threshold. This suggests that there are at least two mechanisms involved in the termination of feeding. There was a gradual fall in the probing threshold in the 24-hour period following blood feeding and the threshold was at a similar level 24 hour after feeding on either blood or 0·5 M sucrose solution. The probing response was not effected by 24 hour rhythms of behaviour and although there were considerable day to day fluctuations in response in a populations of flies kept under laboratory conditions, these fluctuations did not appear to be of a cyclic nature.

Removal of the antennae and the maxillary palps did not significantly alter the probing response to an ammonia concentration of 1·1 mgms per litre. Tarsal lacquering reduced the probing response to ammonia vapour in both antennae-less and normal flies.

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NITROGENOUS WASTE PRODUCTS OF THE TSETSE FLY

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The excrement of tsetse flies has been shown to contain five major constituents, namely uric acid, histidine, arginine, haematin and an as yet unidentified fluorescent yellow pigment. Together these substances make up about 85% of the total dry weight, and when allowance is made for the inorganic salts which must be excreted, they are found to account for the bulk of nitrogenous excretion.

Table 1

The composition of the excrement of male tsetse flies after their third blood meal

	ug/mg dry weight of blood Observed	Expected
Uric Acid	341·6 ± 9·0	371
Arginine	33·1 ± 1·1	35
Histidine	56·3 ± 1·4	69
Haematin	28·2 ± 0·8	26
Pigment	17·6 ± 0·6	—
	476·8	
Total dry weight	564	

Quantitative details of the results are given in Table I, which shows that uric acid is the main excretory product, as in many other insects. The two amino acids together make up about 20% of the total, and this is an unusually high value (2). The occurrence of such large amounts of excretory arginine and histidine is perhaps a reflection of the very high nitrogen content of these substances, which rivals that of uric acid itself. Arginine contains 34% nitrogen and histidine 27%, in contrast to the nitrogen content of other protein amino acids which may be as low as 8% and never exceeds 20%. It would presumably be uneconomical to deaminate substances as rich in nitrogen as these, since any gain which might accrue from the deaminated fraction would be in large part offset by metabolic losses involved in uric acid synthesis. One might therefore suppose that, in the absence of substantial protein synthesis, the arginine and histidine arising as a result of digestion of the blood meal would be quantitatively excreted, while other dietary amino acids would be deaminated and the ammonia detoxicated by incorporation in uric acid. Knowing the amino acid composition of blood proteins it is possible to estimate how much arginine, histidine and uric acid should, on this view, be excreted per mg of blood ingested. Such estimates are shown in column 2 of Table 1. They are naturally subject to considerable error associated with variations in the composition of human blood, but the agreement with values for the observed excretion is reasonably close. Estimates of the amount of haematin taken in with the blood meal have been included, and the results suggest that this substance also is quantitatively eliminated.

The data of Table 1 are of interest in showing that for every mg dry weight of blood ingested more than half of a mg must be excreted in order to dispose of the nitrogen. When it is considered that the synthesis of a complex molecule like uric acid will involve the expenditure of considerable energy, it is apparent that the net gain of energy to the insect is represented by something very much less than 50% of the blood meal. It would seem that the combination of a blood sucking habit with a uricotelic excretory metabolism is far from ideal.

The rate of excretion of uric acid was found to vary enormously depending on the size of the blood meal. On the first day after feeding the coefficient of regression of the quantity of uric acid excreted on dry weight of the blood meal was $+0{\cdot}175 \pm 0{\cdot}054$, and on the second day $+0{\cdot}108 \pm 0{\cdot}041$. This increase in the rate of excretion with increasing size of blood meal presumably reflects an increase in the rate of digestion, and recalls the observation of a correlation between the amount of ingested blood and protease activity in the gut of *Aedes aegypti* (1).

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THE EFFECT OF *TRYPANOSOMA RANGELI* TEJERA ON THE CONCENTRATION OF AMINO ACIDS IN THE HAEMOLYMPH OF *RHODNIUS PROLIXUS* STÅL

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Trypanosoma rangeli is unlike other parasitic protozoa in that it is not pathogenic to its vertebrate host (man) but damages its arthropod vector; this is the result of penetration by its flagellates of the gut wall of its host *Rhodnius prolixus* and their multiplication in the haemocoelomic cavity. Grewal (1957, Exp. Parasitol., 6: 123-30) showed that this growth inhibited the moulting of *Rhodnius* nymphs and produced a marked swelling of the insect's abdomen. Harington at the same time (personal communication) showed that similar changes occurred if uninfected *Rhodnius* nymphs were fed through a membrane on mixtures of aminoacids.

Grewal and I therefore decided to investigate the amino acids of normal and infected 5th instar nymphs using ion exchange chromatography by the method of Moore and Stein, but we achieved only 2 satisfactory analyses on infected bugs and none on normals. These analyses compared with subsequent analyses for normal bugs showed that taurine, aspartic acid, glycine, alanine, leucine and *iso*leucine were present in greatly increased amounts, but tyrosine, phenylalanine and lysine were decreased below the level of sensitivity of the method. Serine was present as a trace indicating that it too was reduced while threonine, glutamic acid, proline and valine were at the same level as in normal bugs.

A Technicon AutoAnalyser has increased the accuracy to an error of less than 5% but the sensitivity, although increased 10 fold, is not sufficient for analysis of the haemolymph of individual bugs except for the highest peaks. Pooled samples from at least 4 bugs have therefore been used, and because different bugs take up different amounts of blood it has been difficult to establish standard conditions for study of amino acid changes during infection.

Comparison of normal 5th instar nymphs taken 7 days after the blood meal with others taken 14 days after the blood meal showed that between the two periods a general fall in amino acid levels occurred, except in the case of taurine and cystine which increased 10 fold in concentration in one experiment but by smaller amounts in another. Arginine and an unidentified amino acid, probably ethionine, also showed variability in concentration in uninfected bugs.

The original strain of *T. rangeli* used in 1955 produced a massive progressing infection in the haemocoel of 5th instar *Rhodnius*, completely inhibited their moulting and ultimately killed them; but when the work was repeated this year the only strain available failed to produce the original massive infection. The heaviest infection with the new strain occurred after 7-10 days when 5-10 flagellates per low power field were seen; at 14 days, infection levels of less than one flagellate per field were seen and some bugs moulted in the normal way having presumably overcome their infection.

The following tentative conclusions about the behaviour of amino acids in 5th instar *Rhodnius* infected with *T. rangeli* are proposed:—(1) aspartic acid levels are uniformly raised during and after infection, 10 fold with light and 100 fold with massive infection, and this does not appear to be influenced by the nutrition of the bug. (2) glycine, alanine, *iso*leucine and leucine increase 5 fold during a light infection, 10 fold in a massive infection but leucine returns to its normal 14 day level after the infection has been overcome. (3) tyrosine, phenylalanine and histidine varied widely and unpredictably but were reduced below the level of sensitivity in massive infections.

Protein analyses by high voltage electrophoresis on agarose can easily be performed on single bugs throughout an infection. Differences have been shown by this technique between normal 5th instar *Rhodnius* and individuals infected with *T. rangeli.*

ELECTRON TRANSPORT ENZYMES IN THE GROWING AND AGING MOSQUITO

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The energy reserve of the mosquito as reflected by lipid content is dependent on the nutritional status, the mosquito population, the sex, the larval rearing temperature, and the developmental stage (9, 5, 8, 3). These data formed the basis of our hypothesis that the energy requirements and the underlying biochemical reactions for energy utilization vary according to the developmental stage.

Our attention was directed to an investigation of the different pathways of electron transport. These pathways are integrated sequences of biochemical reactions that include the cytochromes and oxygen. They differ, however, in their efficiency to produce ATP, the biochemical form of readily available energy. The relationship of each pathway to total energy production and to developmental stage has not been elucidated.

Previous studies have been concerned with enzymes representing only one pathway of electron transport and with organisms from a short developmental time span (6, 7, 1).

The mosquito is well-suited as an experimental organism for the study of growth and aging. Advantages include discrete developmental stages, rapid and separate growth and aging periods and established nutritional requirements.

The objectives of our study were to determine quantitatively reduced nicotinamide adenine dinucleotide- (NADH-), succino-, and reduced nicotinamide adenine dinucleotide phosphate- (NADPH-) cytochrome *c* reductase and cytochrome oxidase activities in samples of mosquitoes ranging in age from first instar larvae to aged adults. In addition, related enzymes were determined, e.g. pyridine nucleotide transhydrogenase and NAD pyrophosphatase. These enzymes can control the concentration of NADH and NADPH which are essential coenzymes for the previous reactions (2, 3).

MATERIALS AND METHODS. *Aedes aegypti* were grown and aged under standardized conditions. Samples of known age were homogenized and analysed for enzymatic activity. The optimal conditions for maximal enzymatic activity were established, such as pH, reaction kinetics, and substrate specificity. Specific inhibitors of electron transport, antimycin A and amytal, were used to verify the reactions.

RESULTS. Initially some biochemical criteria of growth were determined and included RNA, DNA, and protein content. Maximal values of all parameters were attained at the 4th larval instar. The concentration of protein and DNA remained constant through senescence. These results indicated that protein or DNA content would be a suitable basis for the expression of specific activity of enzymes.

Different age-wise profiles of the various enzymes were observed. The specific activity of NADH-cytochrome *c* reductase was relatively high in the larva, dropped in the pupa, and increased several fold in the adult. NADPH-cytochrome *c* reductase was high in the larva and decreased to a very low value in the pupa where it remained throughout adulthood. The specific activity of the NADH-enzyme in the larva was two times greater than the NADPH-enzyme. Succino-cytochrome *c* reductase was very low in the larva and pupa and increased during the adult stages to a level about 1/5 that of NADH-cytochrome *c* reductase. The profile of cytochrome oxidase was similar to that of succino-cytochrome *c* reductase but was displaced upwards. The actual concentration of this enzyme was at least 3 to 4 times higher than any of the other reductases. Other results indicated that the differences in activity were due to changes in apoenzyme concentration rather than enzyme latency, mitochondrial permeability, or the presence of inhibitors or activators.

Pyridine nucleotide transhydrogenase could not be demonstrated in any stage of the mosquito, but a low concentration of NAD pyrophosphatase was observed.

DISCUSSION. The cytochrome *c* reductase of highest activity throughout the life span of the mosquito is NADH-cytochrome *c* reductase. This enzyme together with cytochrome oxidase represents the electron transport pathway of highest efficiency in the production of ATP yielding a P/O ratio of 3. By comparison, the succino-cytochrome *c* reductase pathway results in a P/O ratio of 2, and the NADPH-cytochrome *c* reductase, a P/O ratio of zero. The succino-

enzyme level is very low in the larva but increases in the adult. These data suggest that only the most efficient pathway, the NADH-enzyme system, is active in the larva, whereas both NADH- and succino-enzymes are active in the adult.

The high NADPH-cytochrome *c* reductase activity in all larval stages is consistent with its role as a generating system to produce NADP required by biosynthetic reactions. This is correlated with the fact that growth occurs only during the larval stages.

The absence of pyridine nucleotide transhydrogenase and the low concentration of NAD pyrophosphatase eliminates these enzymes as significant control mechanisms.

An increase in cytochrome reductase and oxidase activities and thus energy producing potential occurred during aging. One interpretation is that the aged mosquito becomes less efficient in ATP production and, therefore, requires more enzyme to produce the same amount of ATP. Another possibility is that the ATP and energy demands of senescence are increased.

In summary, age-wise profiles of electron transport enzymes representing several pathways were determined and were correlated with developmental status. Pyridine nucleotide transhydrogenase and NAD pyrophosphatase are unlikely control mechanisms for these enzymes

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AUTOGENY IN JAMAICAN "SANDFLIES" (CERATOPOGONIDAE)

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There are three main nuisance species of biting Ceratopogonidae ("sandflies") in Jamaica, *Culicoides furens* Poey, *Culicoides barbosai* Wirth and Blanton, and *Leptoconops bequaerti* Kieffer. Both the *Culicoides* breed in mangrove swamps, but larvae of *L. bequaerti* are found in permanently damp white sand areas, usually within a few yards of the sea.

All three species are autogenous, though there is a possibility that *L. bequaerti* may in fact exist as two races, with only one of these exhibiting autogeny. The ability to produce eggs autogenously is clearly of fundamental importance in biting insects, for at least the following reasons. (i) A high population can be maintained in the absence of hosts. (ii) Rapid colonisation and most effective use of breeding sites is facilitated. (iii) Mortality resulting from flight to the host and back to the breeding ground is eliminated.

Five populations of *C. furens* and two populations of *C. barbosai* were examined for autogeny by means of simple emergence traps. Both *barbosai*, and three of the *furens* populations showed high incidences of autogeny, and in only one of these populations (*furens*) was the proportion below 70% autogenous. The remaining two *furens* groups were both 100% anautogenous. All the autogenous populations came from typical mangrove swamp localities, subject to tidal influence, whereas the wholly anautogenous *furens* populations came from slightly unusual sites that would not be influenced by tide. Tidal inundation might prolong the larval stage, leading to greater fat body accumulation and subsequent autogeny.

The situation in *L. bequaerti* was investigated initially by pupal collections from different breeding sites. Widely varying percentages of autogeny were discovered in the resulting adults, and the wing length distributions were found to be skewed or bimodal in both males and females. Interestingly, within any single population only the smaller females were autogenous.

Attempts were made to understand this phenomenon by rearing larvae of known parentage at different densities, in different sands, and on different breeding sites. Though not completely conclusive, the results of these experiments strongly support the belief that there are probably two races of *L. bequaerti*, one small and autogenous, the other large and anautogenous. Without carefully controlled laboratory experiments, (impossible at present), involving cross-mating between the two groups, a final answer will be very difficult to obtain. From a practical standpoint it is worth noting that although a proportion of the autogenous females do survive the first laying, they probably contribute very little to the biting nuisance.

Females of all three species considered here emerge from the pupa with eggs already developing in the ovaries. The developmental stages reached by the follicles at emergence are respectively: *C. furens*—IIA and IIB, *C. barbosai*—IIB and III, and *L. bequaerti*—early IV. Probable minimum times to laying, in the same order are—60-80 hours, 50-70 hours, and 30-48 hours. *C. barbosai* matures many more eggs autogenously than with a blood meal, and may be progressing towards secondary loss of the bloodsucking habit, though autogenous females survive laying, and will bite viciously given the opportunity.

REPRODUCTIVE HORMONES OF THE HOST CONTROLLING THE SEXUAL CYCLE OF THE RABBIT FLEA (*SPILOPSYLLUS CUNICULI* DALE)

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Maturation of the female rabbit flea, egg-laying and the accelerated defaecation rate associated with maturation can be induced by injecting the host, a castrated male rabbit, with adrenocorticotrophic hormone ("Acthar", Armour Pharmaceutical Co. London) hydrocortisone ("Hydrocortisyl", Roussel Laboratories, London) cortisone ("Cortisyl", Roussel Laboratories, London) and massive doses of oestradiol ("Oestroform", British Drug Houses, London). Some ovarian development and enlargement of the salivary glands can be induced by injections of the thyrotrophic hormone ("Actyron", Ferring AB, Malmo) and thyroxine ("Eltroxin", Glaxo Laboratories, England). On a rabbit weighing 8 lbs. twice as much cortisone is required (1·3 mg. daily for 3-7 days) to produce maturation of the fleas, as on a 4 lb. rabbit (·6 mg. daily for 3-7 days).

The male flea is also under the control of the hormones, and accelerated feeding, and hypertrophy of the mid-gut epithelium can be observed. The defaecation rate of the male flea lags somewhat behind that of the female flea, reaching a maximum of one faecal pellet passed every four minutes.

The rabbit flea is more sensitive to hydrocortisone than to cortisone and will mature in response to doses of 10 micrograms injected daily for 3-7 days into a 10 lb. castrated male rabbit, whereas the minimum dose of cortisone required is 1·3 mg. On these small doses of cortisone maturation and hypertrophy of the mid-gut lining is observed, but the defaecation rate may not be increased beyond one faecal pellet every fifteen minutes.

Fleas sprayed externally (Rothschild and Ford, Nature, 203: 210, 1964) with hydrocortisone or oestradiol, will also mature, feeding on castrated male rabbits and virgin doe rabbits. It was thought possible that fleas could introduce sufficient hydrocortisone on their mouthparts to affect the rabbit itself. Fleas were therefore sprayed and allowed to feed for three to four days on the host. They were then replaced by unsprayed fleas. These unsprayed fleas did not develop. This experiment was repeated and subsequently one matured flea out of the fifty unsprayed fleas was noted. This single specimen may have been overlooked when the first batch of sprayed fleas was removed from the rabbit, but on the other hand hydrocortisone could have been transferred to the rabbit's skin by one of the sprayed fleas, and then ingested by one of the unsprayed replacements.

So far our experiments indicate that during the last ten days of the rabbit's pregnancy, the blood levels of the corticosteroids and oestrogens—under the control of the hormones of the anterior pituitary—are raised sufficiently to initiate and maintain maturation of the rabbit flea and accelerated defaecation of both sexes.

It was discovered during the course of the experiments that maturation of the rabbit flea will occur if the host is affected by myxomatosis. Partial maturation can be induced on rabbits of both sexes and all age groups by intradermal injections of ·2 ml. of live fibroma vaccine ("Weyvak" myxomatosis vaccine, Mansi Laboratories). This is probably an indication that the host reacts to the stress of the virus infections by an increased secretion of corticosteroids.

REPRODUCTION IN THE EUROPEAN RABBIT FLEA AND ITS DEPENDENCE UPON THE REPRODUCTIVE STATE OF THE HOST

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The rabbit flea, *Spilopsyllus cuniculi* (Dale), attained economic significance when it became apparent during 1954 that it was an important vector of myxomatosis in Great Britain. Despite its abundance on the wild European rabbit little was known of the biology of this flea and studies were hampered initially when it proved impossible to culture in the laboratory by the techniques used successfully for several rodent fleas. When rabbit fleas were kept on caged, non-pregnant rabbits no eggs or larvae could be found in the debris accumulating beneath the rabbits. Even when gravid fleas, taken from a shot wild rabbit, were placed on a laboratory rabbit the fleas failed to lay eggs and their ovaries regressed. *S. cuniculi* was first bred in the laboratory in 1960 when eggs and larvae were found among the 5-day-old nestlings in the maternal nest of a doe rabbit on which unfed virgin fleas had been released during its pregnancy.

Subsequently the reproductive biology of the rabbit flea was studied by examining the reproductive organs dissected from female fleas which had been kept for varying periods on test rabbits. The rabbits used were selected to be representative of different reproductive states, e.g. males, non-pregnant, pregnant and recently post-partum females and young of various ages.

Each ovary of the rabbit flea consists of five or six panoistic ovarioles and a criterion for degree of ovarian development is the length of a proximal oocyte follicle (i.e. one adjacent to the oviduct). When several fleas were taken simultaneously from a host their ovaries were all in a similar developmental condition. The ovaries of fleas kept for up to 300 days on non-pregnant female or male rabbits remained immature. On a pregnant rabbit ovarian development commenced about 7 days pre-partum and the proximal oocytes were mature at the time of the host's parturition. A typical series of results is shown in fig. 1. It is postulated that the rabbit, during the final week of pregnancy, provides the fleas with a "factor" essential for ovarian development. Soon after parturition many fleas dropped from the doe into her nest and copulation occurred whilst the female fleas were feeding avidly on the new-born rabbits. The spermathecae of fleas remaining on adult hosts, even pregnant and post-partum ones, never contained spermatozoa. Oviposition occurred in the nest and fleas laid eggs for up to 14 days. Fleas remaining on the post-partum adult did not lay eggs and their mature ovaries regressed. Ovaries of immature fleas placed on an immediately post-partum rabbit did not develop and it is concluded that the factor is absent after parturition. Immature fleas released among nestling rabbits up to 7 days old matured their ovaries in about 2 days, suggesting that such nestlings also provide the factor.

As a result of this reproductive pattern fertilised eggs are laid principally in the maternal rabbit nest. These nests, the only ones made by wild rabbits, provide a warm, moist microclimate and contain dried rabbit-blood, both essential for larval development.

(For further details see Mead-Briggs, A. R., 1964, J. Exp. Biol., 41: 371-402.)

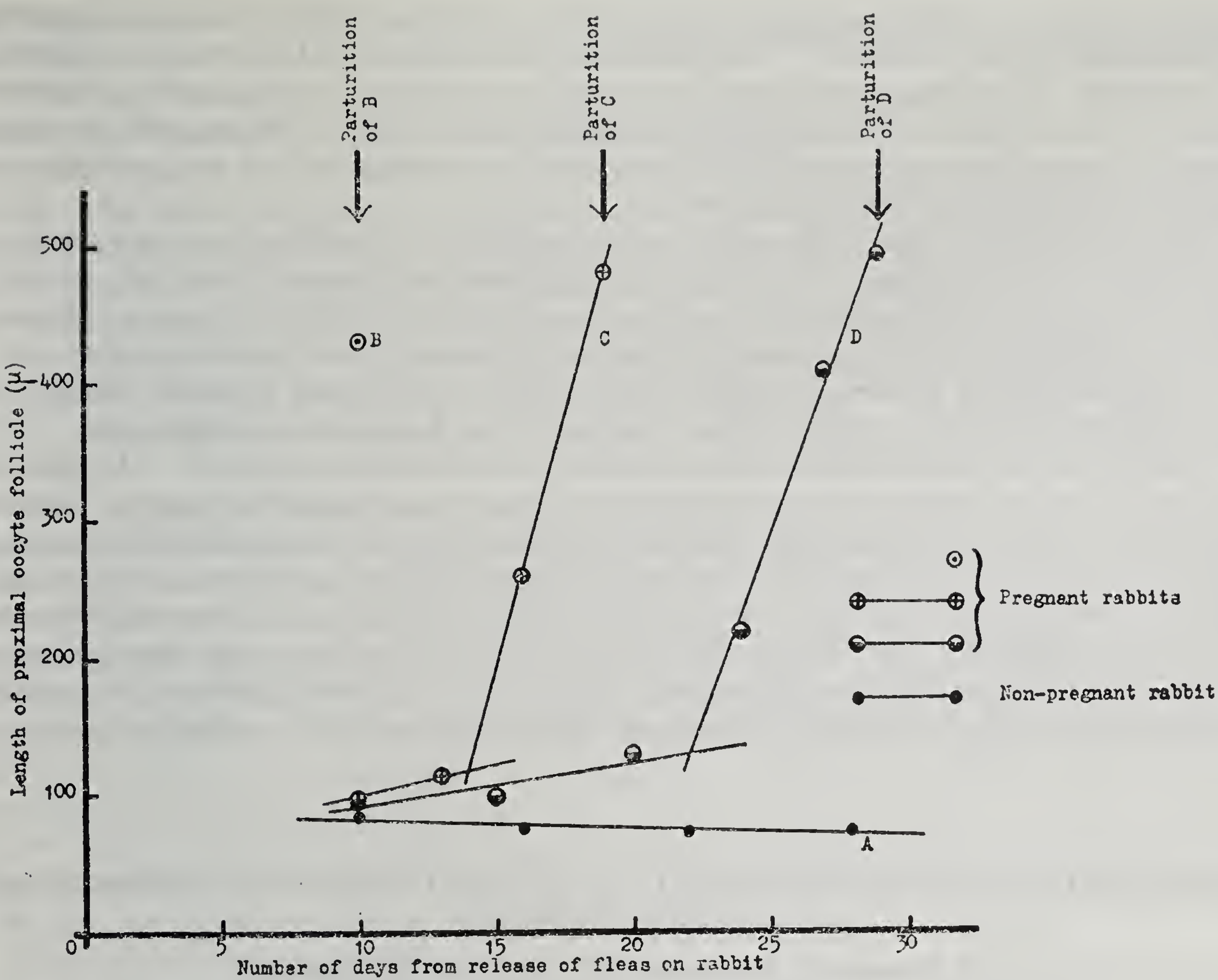

Fig. 1. Ovarian development of rabbit fleas.

CHEMICAL CONTROL OF ARTHROPODS OF MEDICAL IMPORTANCE

RECENT DEVELOPMENTS IN THE CONTROL OF ARTHROPODS OF MEDICAL IMPORTANCE

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The use of residual contact insecticides has been responsible for considerable achievements in the control of Arthropods of medical importance during the last two decades. However, some difficult problems are outstanding. Thus, there are some areas where in spite of thorough and regular coverage of houses with residual insecticide the interruption of transmission of malaria has not been achieved.

Failure to obtain adequate vector control may be due to a number of contributory factors. The two main ones probably are, firstly a lack of vital knowledge of the vector concerned, and secondly the development of resistance to insecticides. What is being done or can be done to overcome these problems?

Obviously more information is required on the normal behaviour of vectors and on any changes in behaviour in the presence of insecticides.

Another approach is to look for new chemicals, and particularly different classes of

chemicals, with the required insecticidal activity that can be used without hazard to spraymen or occupants of treated premises. The World Health Organisation Collaborative Scheme for the evaluation of candidate compounds for use in international public health programmes, initiated five years ago, has examined more than 900 compounds. The majority are organophosphorus compounds or carbamic acid esters, and the more promising are now undergoing evaluation in the field against different vectors.

The search for new chemicals should not be carried out in isolation, and new methods of control must be investigated. The W.H.O. Collaborative Scheme is, in fact, part of an overall programme which includes the introduction of test-kits to check changes in tolerance of vectors to insecticides, and the promotion of the development of novel methods of control.

A new method of utilising a volatile insecticide is the residual fumigant technique by which dichlorvos (DDVP) vapour is slowly released from liquid or solid dispensers.

There is also renewed interest in insect pathogens and biological control. Another form of biological control involves the use of chemicals to cause sexual sterility in insects. Research in the U.S.A. has demonstrated that houseflies and mosquitos can be sterilised by a number of chemicals, and it is now necessary to determine ways in which these chemo-sterilants can be safely employed to control vectors. An extension of the sterilisation technique with intriguing and exciting possibilities is the release of strains of insects with unfavourable genetic factors.

These methods may not offer immediate solution of vector control problems but some have great potentiality either on their own merits or when integrated with established practices.

DONNEES RECENTES CONCERNANT LA LUTTE CONTRE LES MOUSTIQUES ET LES SIMULIES

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Moustiques et simulies sont des diptères nématocères à larves et à nymphes aquatiques dont les femelles sont généralement hématophages. De nombreuses espèces de ces deux familles, du seul fait de leur abondance et de leur agressivité, nuisent au confort et parfois même à la santé des êtres humains. Certaines espèces, en outre, transmettent de graves maladies à l'homme et aux animaux.

L'emploi de plus en plus général, depuis 20 ans, des insecticides à action rémanente, a permis d'entrevoir la possibilité de contrôler ou d'éliminer les espèces indésirables et de grandes campagnes ont été entreprises à cet effet dans tous les continents.

L'apparition, surtout chez les moustiques, de populations résistantes à certains insecticides et le désir de pouvoir lutter sélectivement contre les espèces indésirables sans éliminer la faune commensale ni bouleverser l'équilibre biologique du milieu, ont montré la nécessité de disposer d'une vaste gamme de toxiques appartenant à des groupes chimiques aussi différents que possible les uns des autres et ont stimulé les recherches sur les méthodes de lutte ne faisant pas appel aux insecticides.

Selon les résultats désirés et les conditions d'environnement les insecticides sont employés soit contre les adultes, soit contre les larves, de moustiques et de simulies. La lutte contre les adultes peut être effectuée à l'extérieur ou à l'intérieur des habitations.

L'éxécution de traitements insecticides à l'intérieur des habitations vise exclusivement les moustiques au moins partiellement endophiles et en particulier les anophèles vecteurs du paludisme. La méthode classique consiste à recouvrir périodiquement les surfaces intérieures des batiments d'un dépot de DDT, dieldrine ou de HCH, pour tuer les vecteurs avant qu'ils n'atteignent un âge physiologiquement dangereux. Malheureusement de nombreuses espèces sont devenues résistantes à ces deux insecticides. L'emploi d'insecticides fumigants à action rémanente n'a pas encore été couronné de succès, et les insecticides organophosphorés disponibles pour le traitement des habitations, malathion et fenthion, sont beaucoup moins maniables que le DDT ou la dieldrine.

La lutte contre les adultes de moustiques et de simulies hors des habitations permet de détruire les espèces exophiles et constitue parfois la méthode de choix lorsque les gites larvaires

sont inaccessibles ou d'une étendue telle que leur traitement n'est pas économiquement réalisable.

Pour la destruction des simulies les traitements imagocides sont presque toujours aériens. L'insecticide de choix est le DDT en solution dans le gas-oil.

La destruction des moustiques dans leurs lieux de repos extérieurs vise généralement à protèger des zones habitées et est habituellement basée sur la nébulisation d'insecticides à l'aide de puissants appareils auto- ou aéro-portés. La rémanence du traitement est très faible. Le principal insecticide employé est le malathion, mais le fenthion et le dibrom donnent aussi des résultats très satisfaisants et sont sans danger pour l'homme dans ces conditions d'utilisation.

La lutte antilarvaire peut être entreprise dans une grande variété de situation et pour être efficace doit être étroitement adaptée aux circonstances. Un cas bien particulier est celui de la lutte contre les simulies dont les larves vivent presque exclusivement dans les eaux courantes.

Pour la lutte contre les larves de simulies on doit employer un insecticide toxique pour ces insectes tout en offrant une grande marge de sécurité pour la macrofaune aquatique et pour les mammifères et la rémanence du produit employé est plutôt un inconvénient qu'un avantage. Le DDT reste actuellement le produit le plus utilisé; comme il est insoluble dans l'eau sa formulation doit lui assurer une portée maxima. En fait il sédimente dans les zones sans courant et est susceptible de s'accumuler pendant de longues périodes dans les tissus adipeux des poissons et dans le sol. Dans certaines conditions au moins le remplacement du DDT par d'autres insecticides est souhaitable; le fenthion et le dipterex semblent être les meilleurs insecticides de substitution, mais n'ont pas encore été employés dans des zones tropicales. La lutte contre les larves de simulies, contrairement à certaines craintes, ne semble pas perturber de façon durable l'équilibre biologique des cours d'eau traités, sauf en ce qui concerne les simulies, car seules les portions de rivières contenant des gîtes sont traitées.

Bien que la lutte contre les larves de moustiques soit encore très fréquemment basée sur l'emploi des insecticides organochlorés classiques, une gamme très variée de composés organophosphorés et de carbamates commence à être disponible, permettant presque toujours d'adapter les campagnes aux contigences locales. Les principaux facteurs à prendre en considération pour choisir l'insecticide, la formulation et la méthode d'application sont: la sensibilité des larves aux insecticides, la nature des gîtes, la pollution et le pH de l'eau, l'utilisation ultérieure de l'eau et le degré de protection à assurer à la macrofaune aquatique, et enfin la rémanence souhaitée.

L'apparition de populations de moustiques physiologiquement résistantes aux insecticides a amené l'O.M.S. à coordonner un vaste programme de recherches pour favoriser la découverte et l'évaluation de nouveaux insecticides utilisables en santé publique. Les deux principaux critères de sélection sont l'inocuité pour l'homme dans les conditions probables d'utilisation et la rémanence sur différents types de substrats. L'évaluation finale est faite sur le terrain, dans des maisons-pièges, puis dans des villages et des groupes de villages, sous stricte surveillance médicale. Jusqu' à présent peu de composés ont pu être retenus pour le traitement des habitations, mais beaucoup semblent utilisables pour la lutte antilarvaire et certains se prètent aux nébulisations imagocides. De nombreuses études sont par ailleurs consacrées à l'amélioration des formulations, à la recherche de synergistes et de composés chimiostérilisants.

Actuellement la quasi-totalité des campagnes dirigées contre les moustiques et simulies sont basées sur l'emploi d'insecticides. D'autres méthodes de lutte seront cependant disponibles dans un plus ou moins proche avenir et la prévention de la formation des gîtes larvaires pourrait être l'objet de plus d'attention.

Il apparait de plus en plus que l'avenir est à l'emploi conjoint des insecticides et d'autres méthodes de lutte contre les vecteurs. Un tel controle intégré, comme d'ailleurs l'emploi raisonné des seuls insecticides, nécessite l'étude détaillée préalable de la biologie, du comportement, de la génétique et de la dynamique des populations des espèces à détruire, et nous ne pouvons que nous féliciter de ce que cette manière scientifique d'aborder le problème soit enfin reconnue comme la seule valable. Cela implique que la planification des campagnes soit faite par des équipes d'entomologistes parfaitement au courant des différentes techniques d'étude et de contrôle des vecteurs, ce qui est encore trop rarement le cas actuellement.

RECENT ADVANCES IN THE CONTROL OF TSETSE FLIES

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The present position in practical control is that bush clearing either partial or complete is used less as an overall control measure and mainly now to create barriers to protect fly free areas or to isolate areas where other control measures are employed. Game destruction is used generally only as a last resort, but because it is comparatively inexpensive and is effective if properly employed, it is still used. Ground application of insecticides is used as a routine control measure in many countries. For example, for control of *G. palpalis* throughout East and West Africa, for control of *G. morsitans* and *G. tachinoides* in Northern Nigeria, in combination with other methods for the control of *G. morsitans* in Central Africa and on a smaller scale in Tanganyika for the control of *G. swynnertoni*, *G. morsitans* and *G. pallidipes*.

The following are recent advances:

(*a*) GROUND APPLICATION OF INSECTICIDES. The discriminative application of insecticides has been considerably refined during the past two or three years.

In the Sudan zone of Northern Nigeria the cost has been reduced from £155 to £55 per square mile actually sprayed by the more precise selection of sites to spray. For example in some areas with a very extreme dry season merely spraying of the trunks of large trees in shaded areas up to only two feet from the ground has been sufficient to eradicate *G. morsitans*. In the more extensive habitat in the Northern Guinea zone spraying under more or less horizontal branches over two inches in diameter between five and sixteen feet from the ground on all trees in areas where *G. morsitans* tended to concentrate was effective at a cost of about £400 per square mile of country actually sprayed but further work is in progress to define more precisely the resting sites. (The present technique costs only about £50 per square mile of country reclaimed) (1). The T.P.R.I. experiment in 1958 in similar country in Uganda where the undersides of horizontal branches on one species of tree (*Acacia gerradii*) only were sprayed cost about £250 per square mile (2).

In Tanganyika we have made a statistical analysis of the resting sites of *G. swynnertoni* and on the basis of this treated with dieldrin emulsion the sites which were the preferred resting places, i.e. beneath branches at heights between four and nine feet, of one to four inches in diameter and sloping less than 35° to the horizontal. This eradicated the fly at a cost of £42 per square mile. In Rhodesia insecticide has been applied to bush in restricted areas which are known to be favoured by *G. morsitans* i.e. to resting areas rather than to resting sites themselves and as a routine measure over large areas a reduction of 98% has been obtained at a cost of about £80 per square mile (3). More precise details of the fly habits are required to make this a fully effective method.

Considerable advances have also been made in the study of the persistence of insecticide on bark surfaces and of the effect of, for example, bush fires.

(*b*) AERIAL SPRAYING. This is generally more costly than ground application of insecticide because it has been found impracticable to put down a persistent deposit in the right places from the air and hence 6-8 applications of an aerosol which only kills the adults are required to achieve eradication. It is however a useful method when a rapid reduction of fly over a large area is required, for example to control a sleeping sickness outbreak.

Much progress has been made in reducing the quantity of liquid required and in our latest experiments (4) 1/80 gallon (or 56 ccs) per acre was used compared with $\frac{1}{4}$ gallon in our first experiments in 1949. This minute rate of application allows a light aircraft to cover several square miles in one sortie. This reduction has been achieved by the better atomisation of more concentrated solutions of more toxic insecticides and has reduced the overall cost from £1,000 to about £200 a square mile.

Other advances in the method have been various improved swathe marking techniques of which the most effective has been by the use of Aldis lamps (5), and the tentative use of moonlit nights for spraying under ideal atmospheric inversion conditions. Such use would make greater utilisation of the aircraft possible and reduce the risk of delays in the spraying schedule.

Further improvement is possible in the formulations and dissemination of the insecticide, which still accounts for 60% of the total cost. At present dieldrin 20% solution at 0·0124

gallon per acre costs £200 per square mile, with better atomisation telodrin 20% solution could be used at half the dosage. Endosulfan which is slightly more toxic than dieldrin to tsetse, safer and cheaper, also has possibilities, as has an insecticide such as fenthion which is more toxic to pregnant female tsetse than is dieldrin (6).

(*c*) USE OF STERILE MALES. Our preliminary experiments with the chemosterilants metepa and apholate on *G. morsitans* were not very promising in that although low dosages did not completely sterilise they greatly reduced the life of the flies (7). However a comprehensive investigation is being carried out in Southern Rhodesia on the effect of both radioactive compounds and chemosterilants on tsetse flies and on methods of rearing them in large numbers. The relative effectiveness of different methods of application and of different chemicals on behaviour, vigour and longevity is also being studied.

If it is not possible to rear tsetse economically in sufficiently large numbers it may still be possible to use chemosterilants combined with attractants on resting sites or in traps or for making female flies into booby traps to sterilise males which attempt to mate with them. The work being done on attractants and on traps is therefore relevant to this method of control.

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LABORATORIUMSUNTERSUCHUNGEN ÜBER DIE IRRITABILITÄT EINER NATÜRLICHEN POPULATION VON *ANOPHELES L. ATROPARVUS* GEGENUBER DDT

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Freilandbeobachtungen über das Verhalten von *A. l. atroparvus* in ungespritzten und mit DDT gespritzten Versuchshütten in Norddeutchsland hatten eine offensichtlich jahreszeitlich bedingte Verschiebung der Insektizidwirkung auf die einfliegenden Anophelen gezeigt (2). Es wurde vermutet, dass die zu Beginn der Einwinterung von *A. atroparvus* im Herbst beobachtete absinkende Mortalität und der veränderte Ausflug aus den DDT-Hütten—allein oder zusammen mit anderen Faktoren—auf eine Veränderung in der Irritabilität der Mücken zurückzuführen ist. Zur Prüfung dieser Vermutung wurden 1962 und 1963 jeweils über mehrere Monate Laboratoriumsteste zur Bestimmung der Irritabilität von Weibchen, die am Tage vorher in Schweineställen gefangen worden waren, durchgeführt. Für diese Untersuchungen wurde die von Coluzzi modifizierte WHO-Methode zur Bestimmung der Irritabilität von Stechmücken (1) und 1963 ausserdem der WHO-Standardtest (3) benutzt. Die Teste wurden bei 24-25°C und 60-70% Luftfeuchte ausgeführt. Alle Mücken wurden einzeln getestet.

Bei der Auswertung der Versuche nach der Zeit bis zum ersten Aufflug der Mücken zeigten sowohl die mit der Colluzzi-Methode als auch die mit dem WHO-Standardtest erhaltenen Ergebnisse eine grosse Variabilität. Infolgedessen lassen sich keine signifikanten Unterschiede zwischen den gemessenen Irritabilitätswerten in den verschiedenen Monaten nachweisen.

Bei der Zusammenstellung der Testergebnisse nach der Anzahl der Aufflüge innerhalb von 15 Minuten Beobachtungszeit ergeben sich die in Tabelle 1 aufgeführten Daten.

TABELLE 1
Zahl der Aufflüge von A.l. atroparvus in 15 Minuten (COLUZZI-Methode)

Monat	Versuch	1962				1963			
		Zahl der Weibchen	*Zahl der Aufflüge*		*Mittelwert-differenz DDT/Kontrolle*	*Zahl der Weibchen*	*Zahl der Aufflüge*		*Mittelwert-differenz DDT/Kontrolle*
			Spanne	*Mittel*			*Spanne*	*Mittel*	
Juni	DDT 4%	33	1–33	12,9	8,6				
	Kontrolle	15	0–21	4,3					
Juli	DDT 4%					102	0–67	21,8	12,5
	Kontrolle					52	0–21	8,6	
August	DDT 4%	36	0–53	21,4	13,7	46	0–54	21,5	15,4
	Kontrolle	19	0–20	7,7		24	0–19	6,1	
September	DDT 4%	40	0–45	18,7	15,8	51	0–55	23,9	14,0
	Kontrolle	19	0–11	2,9		26	1–23	9,9	
Oktober	DDT 4%	53	0–42	13,2	10,9	68	2–63	24,1	17,2
	Kontrolle	25	0–12	2,3		33	0–22	6,9	
November	DDT 4%					66	0–66	24,6	16,1
	Kontrolle					32	0–25	8,5	
Dezember	DDT 4%	29	0–33	11,5	9,7	69	1–78	24,0	16,6
	Kontrolle	19	0– 8	1,8		34	0–30	7,4	

Im Jahre 1962 ergibt sich ein Anstieg der Irritabilität von Juni bis September, dem Beginn der Einwinterung von *A. l. atroparvus*, und dann ein Abfall der Werte bis zum Dezember. Im Jahre 1963 hingegen zeigte sich eine monatliche Verschiebung der im Test gezeigten Irritabilität, die nicht in derselben Weise wie im Vorjahre verlief. Besonders im WHO-Standardtest ergab sich ein ganz kontinuierlicher Anstieg. Die Mittelwertsdifferenzen betrugen von Juli bis Dezember 11,5; 14,0; 14,8; 17,1; 17,1 und 18,5. Die monatlichen Differenzen in beiden Beobachtungsjahren erreichen jedoch wegen der grossen Variabilität der Einzelergebnisse keine statistische Signifikanz. Die Aufflüge der Mücken von den Kontrollpapieren waren relativ hoch, besonders im Jahre 1963.

Vergleichsteste mit einer Laboratoriumskolonie, die 1957 mit *A. l. atroparvus* von derselben Lokalität begonnen worden war, zeigten eine deutlich geringere Irritabilitat der Laboratoriumskolonie mit der Coluzzi-Methode und besonders mit dem WHO-Standardtest.

Unter den vorliegenden Versuchsbedingungen konnten die Laboratoriumsteste wohl die Irritabilität der örtlichen population von *A. l. atroparvus* gegenüber DDT zeigen, nicht aber jahreszeitliche Schwankungen in der Irritabilität statistisch signifikant erfassen. Darüberhinaus konnten die in einem Jahre gewonnenen Ergebnisse im folgenden Jahr nicht reproduziert werden.

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FELDBEOBACHTUNGEN ÜBER IRRITIERENDE WIRKUNG VON DDT-BELÄGEN AUF STECHMÜCKEN

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In Ostfriesland (Norddeutschland) wurde die irritierende Wirkung von DDT-Belägen auf natürliche Populationen von *Anopheles l. atroparvus* und *Culex p.pipiens* untersucht. Unsere vorher im Laboratorium ausgeführten Versuche hatten keine befriedigenden Aufschlüsse über die Irritabilität der untersuchten Mückenpopulationen gegeben. Es erscheint zudem zweifelhaft, ob die in solchen Testen gezeigte Irritabilität von Mücken, die in zwangsweisem Kontakt mit dem Insektizid gehalten werden, Rückschlüsse auf deren Verhalten in gespritzten Räumen zuläßt.

Wir haben deshalb die Irritabilität der Mücken unter Bedingungen studiert, die den natürlichen besser angepaßt sind und den Mücken freie Flugmöglichkeiten lassen. Dazu wurden vier Versuchshütten von $2 \times 2 \times 2$ m Größe benutzt, von denen zwei mit DDT 2 g/m^2 ausgespritzt wurden und zwei als Kontrollhütten ungespritzt blieben. Die Hütten hatten jeweils 1 oder 2 Ausflugfallen.

In der ersten Versuchsserie wurden jeweils 100 Weibchen von *A. atroparvus*, die kurz vorher in Schweineställen der Umgebung gefangen worden waren, am Tage in die Versuchshütten freigelassen. Als Folge der irritierenden Wirkung des DDT erschienen schon in den ersten 5 Minuten nach Versuchsbeginn Mücken in den Fallen. Innerhalb einer Stunde flogen aus den DDT-Hütten insgesamt 24% (297 der 1230 eingesetzten Examplare) aus. Davon waren nach 5 Minuten 13%, nach 15 Minuten 41%, nach 30 Minuten 71% und nach 45 Minuten 92% ausgeflogen. Demgegenüber betrug der Ausflug aus den Kontrollhütten insgesamt nur 3% (31 von 1029 eingesetzten Exemplaren), von denen mehr als ein Drittel in den ersten 5 Minuten nach Versuchsbeginn ausflogen.

In einer zweiten Versuchsserie haben wir Mücken aus unseren Laboratoriumskolonien in die Hütten freigelassen. Wir benutzten dazu zwei Stämme von *A. atroparvus,* die mit Mücken der lokalen Population aufgebaut worden waren. Einer dieser Stämme war über 27 Generationen unter DDT-Druck gehalten worden und hatte eine 4-fache DDT-Toleranz entwickelt. Überraschenderweise zeigten beide Stämme, weder bei den DDT- noch bei den Kontrollhütten, einen Ausflug in die Fallen. Offensichtlich hatten diese Stämme durch die langjährige Laboratoriumszucht einen Teil ihrer natürlichen Irritabilität verloren.

Außerdem wurden auch Mücken eines DDT-sensiblen Laboratoriumsstammes von *A. stephensi* in die Hütten freigelassen. Im Vergleich zu *A. atroparvus* zeigte dieser eine hohe Irritabilität. Aus den DDT Hütten flogen 57%, aus den Kontrollhütten dagegen keine der jeweils 100 eingesetzten Weibchen aus.

Einen sehr hohen Ausflug aus den DDT-Hütten zeigte auch die örtliche Population von *Culex pipiens.* Von den eingesetzten Weibchen verließen 76% die DDT-Hütte. Dieser Ausflug kann jedoch nur zu einem Teil auf Irritabilität zurückgeführt werden, da auch der Ausflug aus den Kontrollhütten mit 51% sehr hoch war.

Bei den Freilassungsversuchen mit Mücken der Freilandpopulation von *A. atroparvus* war aufgefallen, daß ein Teil der irritierten und in den DDT-Hütten unruhig umherfliegenden Mücken offensichtlich durch das durch die Fallen einfallende Tageslicht am Ausflug aus den dunklen Hütten gehindert wurde. Deshalb wurden in einer weiteren Versuchsserie wiederholt je 100 Weibchen von *A. atroparvus* abends, zur Zeit der natürlichen Aktivität, in die Hütten freigelassen und der Ausflug am nächsten Morgen ausgewertet. Es zeigte sich, daß aus den DDT-Hütten 38% von 2007 und aus den Kontrollhütten 34% von 1447 eingesetzten Weibchen während der Nacht in die Fallen ausgeflogen waren. Bei dieser Versuchsanordnung wurde die Irritabilität also durch den hohen natürlichen Ausflug der Mücken verdeckt.

Bei der Bewertung der Ergebnisse dieser Freilassungsversuche muß darauf hingewiesen werden, daß der Ausflug immer wesentlich niedriger war als bei Mücken, die natürlicherweise in die Versuchshütten eingeflogen waren. Von den natürlicherweise eingeflogenen Weibchen von *A. atroparvus* verließen 57% von 1050 die DDT-Hütten in derselben Nacht, in der sie eingeflogen waren, im Vergleich zu 8% von 1384 bei den Kontrollhütten (1). Für *Culex pipiens* betrugen die entsprechenden Ergebnisse 97% von 4732 und 94% von 3305 eingeflogenen Weibchen.

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RESULTATS D'UNE CAMPAGNE LARVICIDE CONTRE *SIMULIUM DAMNOSUM* THEOBALD (*DIPTERA-SIMULIIDAE*) EN AFRIQUE DE L'OUEST

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Section Onchocercose, Bobo Dioulasso, Hte. Volta

La zone pilote du haut-bassin de la Volta Noire, mise en expérimentation en 1961, avait pour but d'effectuer un traitement larvicide contre *Simulium damnosum* dans une zone assez vaste et relativement bien isolée.

Cette région, située à la limite de la savane guinéenne et de la savane soudanienne, présente les caractères suivants: 1.200 mm de précipitations annuelles, cours d'eau permanents, végétation du type savane boisée faisant place, le long des cours d'eau, à la galerie forestière.

La prospection intégrale du bassin de la Volta Noire dans sa partie amont ainsi que des bassins adjacents de la Comoë et du Farako a été effectuée afin de déterminer exactement l'emplacement des gîtes préimaginaux de l'espèce; de très nombreux gîtes ont été décelés, en toutes saisons, sur les fleuves principaux, leurs affluents et de nombreux sous-affluents. Simultanément, des captures de femelles nous ont permis de mettre en évidence deux couloirs de réinfestation entre la Volta Noire, la Comoë et le Farako.

Traitement insecticide:

Le traitement de cette zone a été effectué selon la méthode classique des épandages larvicides contre les Simulies. Les élevages effectués au laboratoire nous ont permis de choisir des intervalles de 10 jours entre les traitements.

La série d'épandages s'est échelonnée de Novembre 1962 à Février 1963, l'impraticabilité des pistes d'accès interdisant le traitement en saison des pluies.

Les deux bassins hydrographiques pouvant provoquer une réinfestation de la Volta Noire ont été maintenus sous traitement durant 13 mois.

L'insecticide utilisé a été le DDT en solution émulsifiable à 30% (densité: 0,965) dosé à une partie par million dans le courant. La diminution constante du débit des cours d'eau nous a amenés à effectuer extemporanément de fréquentes mesures de débit en chaque point d'épandage et, la solution insecticide ayant une moindre portée dans les rivières à faible débit, à multiplier ces points d'épandage.

350 km. de cours d'eau ont été traites, ce qui represente 40 points d'épandage.

Afin de contrôler l'effet du traitement, les séries de captures hebdomadaires effectuées sur toute la zone depuis Juillet 1961 ont été poursuivies. D'autre part, une surveillance constante de nombreux gîtes préimaginaux a été effectuée par les responsables des épandages.

Resultats:

Nous n'avons pu capturer aucune femelle ni récolter aucune forme préimaginale dans les deux bassins de contact; le bassin de la Volta Noire était donc à l'abri de toute réinfestation par l'extérieur.

Immédiatement après le traitement, la disparition complète de l'espèce a pu être observée dans ce dernier bassin, sauf en un petit foyer localisé au centre de celui-ci, ce qui nous a obligé à prolonger les traitements au-delà des limites normales.

En saison des pluies, par dissémination des femelles autour de ce foyer refractaire, une grande partie de la zone a été réinfestée. Durant la saison sèche suivante (Novembre 1963-Mai 1964), nous avons constaté, sans traitement supplémentaire, une regression de la population de *S. damnosum*, qui s'est de nouveau restreinte au foyer précédemment mentionné. Une expérimentation actuellement en cours concernant cette disparition nous a permis de constater que l'insecticide modifie tres profondément, parfois à longue échéance, l'équilibre biologique des cours d'eau traités.

Les captures effectuées avant, pendant, et après la campagne larvicide, ainsi que les captures témoin entreprises en dehors de la zone traitée, nous ont fait estimer la diminution de population à 85% durant les 18 mois suivant le traitement.

COMPARISON OF AERIALLY DISPERSED WATER AND OIL FORMULATIONS OF DIBROM AND MALATHION FOR CONTROL OF ADULT *AEDES TAENIORHYNCHUS*

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This paper is a report of field trials conducted in the United States of America in the State of Florida, to obtain data on the relative efficacy of aerially dispersed water emulsions and oil solutions of two organo-phosphorus insecticides, Dibrom (dimethyl 1,2-dibromo-2 2-dichloroethyl phosphate) and malathion (o,o-dimethyl dithiophosphate of diethyl mercaptosuccinate) for control of adult *Aedes taeniorhynchus.* Personnel from the U.S. Army Environmental Hygiene Agency, ACC, Maryland, and the U.S. Air Force Special Aerial Spray Flight, Langley Air Force Base, Virginia, actively participated, in conjunction with personnel of the USDA Laboratories, Gainesville, Florida, in conducting the field tests reported in this paper.

The test sites, formulations tested, toxicant dispersed per acre, and test results are presented in Table 1.

The test data would indicate that water emulsions and fuel-oil solutions of malathion and Dibrom were about equally effective in abatement of adult *Aedes taeniorhynchus* for periods extending up to 6 hours following treatment of test plots.

Both formulations of malathion achieved excellent control of *A. taeniorhynchus* for 24 hours following aerial spraying.

Oil solutions of Dibrom applied at 0·1 pound of toxicant per acre achieved excellent control of *A. taeniorhynchus* for 24 hours following treatment of test plots. Oil solutions of Dibrom at a dosage of 0·05 pound of toxicant per acre gave fair control of *A. taeniorhynchus* after 6 hours, but failed to yield satisfactory control 24 hours following treatment.

Water emulsions of Dibrom applied at a dosage of 0·1 pound of toxicant per acre gave excellent control of *A. taeniorhynchus* after 6 hours, but conflicting results were obtained in depression of pretreatment landing counts 24 hours following treatment.

Summary. Excellent control of adult *Aedes taeniorhynchus* was obtained with both water and oil formulations of malathion in aerial spray tests conducted in Florida.

Water emulsions and oil solutions of Dibrom applied at 0·1 pound of toxicant per acre achieved excellent control of test mosquitoes for 24 hours in two test areas, but failed to achieve adequate control in a third test site.

The test data, while preliminary in scope, would suggest a promising future for use of both water emulsions and oil solutions of organophosphorus insecticides in aerial spray programs.

TABLE 1

Efficacy of aerially dispersed water emulsions and fuel-oil solutions of malathion and Dibrom for control of adult *Aedes taeniorhynchus*

Test Sites County	*Insecticide Formulation*	*Toxicant-lbs./acre*	*Pretreatment Landing Counts*[1]	% *Reduction in Landing Counts*[2] 3 *Hrs.*	6 *Hrs.*	24 *Hrs.*
Lee	Malathion-Oil	0·25	52	88	88	88
Volusia	Malathion-Oil	0·33	72	86	90	89
Brevard	Malathion-Oil	0·33	88	73	99	84
Volusia	Malathion-Water	0·33	56	81	90	96
Brevard	Malathion-Water	0·33	19	92	100	89
Volusia	Dibrom-Oil	0·05	32	81	80	35
Brevard	Dibrom-Oil	0·05	124	49	84	63
Lee	Dibrom-Oil	0·1	70	95	95	90
Volusia	Dibrom-Water	0·1	97	89	88	20
Brevard	Dibrom-Water	0·1	107	88	98	92

1. Average number of mosquitoes landing per man for one minute.
2. Data corrected with Abbott's formula for population changes in untreated control plots.

THE POTENTIAL USEFULNESS OF SYSTEMIC INSECTICIDES IN A CATTLE GRUB ERADICATION PROGRAM

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Attempts to eradicate cattle grubs (*Hypoderma lineatum* (de Villers) and *H. bovis* (Linnaeus)) from any extensive area have met with only limited success. Simple but very effective control measures such as destruction of individual larvae by hand methods have been used in several long-term European campaigns, e.g., those in Denmark, Germany and Switzerland. In Great Britain, Canada and the United States the systematic application of rotenone was used to effect drastic reductions in grub numbers but none of these programs resulted in eradication. The reasons for failure are undoubtedly complex but it is significant that in all countries livestock owners lost interest as soon as the number of grubs was drastically reduced.

It was hoped that the much greater efficacy of animal systemic insecticides would make it feasible to eradicate *Hypoderma* from circumscribed areas by their use. Under optimum conditions of application several compounds can be used to effect virtually 100% control. Since there is only one generation per year to cope with, in theory it should be possible to reduce populations to such a low point in one or two years that they would no longer be self-sustaining. Two significant experiments in North America have tested this theory.

In 1957 Rich initiated a trial in a semi-isolated area in British Columbia (2). He used a range herd of beef cattle (1,200 to 1,600 head) that was separated from all other cattle by at least 10 miles of mountainous terrain. The cattle were treated with ronnel the first three years of the test and with Ruelene R for the next three years. The following reductions in grub infestations were observed: 1957 - 76·8%; 1958 - 89·0%; 1959 - 87·5%; 1960 - 91·7%; 1961 - 91·0% and 1962 - 100%. Because of the effectiveness of the 1962 treatment, the cattle were not treated in 1963. The average number of grubs per untreated animal follows: 1957 - 30·2; 1958 - 14·5; 1959 - 1·6; 1960 - 2·5 1961 - 2·7; 1962 - 0·2; 1963 - 1·7. The reasons for the increase in 1963 are not fully understood but it is obvious that eradication was not achieved in 1962 although it was closely approached.

A later test in a more isolated locality was initiated in 1960. Riehl *et al.* (1) applied Ruelene dermally to all the cattle on Santa Rosa Island, an island 54,000 acres in size located about 30 miles off the coast of California. After four years of treatment grub counts declined to zero in 69 untreated calves and to one grub in 977 treated cattle.

In less isolated localities eradication can be expected to be more difficult to achieve. However highly acceptable ectoparasite control programs can be devised which will require multiple applications of systemic insecticides for the control of other species but will eliminate cattle grubs as a secondary benefit or at least reduce them to a very low level. The possibility of releasing sterile males to complete the eradication process should be considered. Attractants for use in trapping unmated females of *Hypoderma* should be sought as their use might furnish a means of eliminating the last survivors of a population.

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CONTROL OF VECTORS OF PUBLIC HEALTH IMPORTANCE IN HUNGARY

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Control of epidemiologically significant public health insects was launched after the Second World War. This was due, of course, to the appearance of DDT and similar insecticides. The first measures were directed against vectors of malaria and typhus. Reduction of house-flies is a considerable problem, as is the control of biting flies such as mosquitoes, sandflies, midges, etc.

A campaign against *Anopheles* in 1949, financially supported by the Ministry of Health and UNICEF, was the first large scale control of these insects in the country and half a million people were protected. There are now no reported cases of endemic malaria, which is of especial interest because of the intensive rice production and irrigation in certain parts of the country. Mihályi and Sztankay have published an account of the Hungarian Culicidae and methods for their control.

Mosquito control is partially by elimination of breeding sites or their treatment with contact insecticides, but extermination of adults is more widely practised using DDT, BHC and organophosphorous derivatives as dusts and sprays on vegetation. Good results have been obtained from fogging, using the swing-fog, heat aerosol machine, but dusting from aeroplanes is too expensive although the results are good.

Culicoides and Simuliidae regularly cause a serious problem; the larvae of the former can be controlled in the field by applying 10% DDT and 10% diazinon in a dilution of one part per million. As dusts and for fogging, both DDT and BHC are effective against larvae and adults.

Another programme of an essentially sanitary nature is the control of house-flies etc. which breed prolifically in the climate and with the methods of animal husbandry in use. Control is based first on sanitary measures and secondly on chemical methods, including spraying of walls and the use of baits containing insecticides. Striking results have been achieved by the use of insecticide-impregnated strips in houses, stables, piggeries, etc., each strip being 40×5 cms., one for every two square metres. No DDT was used in dairies or food processing establishments. Owing to increasing DDT resistance it is necessary to use mixtures of a chlorinated hydrocarbon and organophosphorous compounds, or the latter alone.

Much attention is paid to lice control, although stringent sanitary regulations have resulted in the reduction of the problem. The insecticide used is a powder containing 10% DDT. Studies of resistance have shown the presence of vigour tolerance in some strains and also one case of DDT resistance. As a result a spray containing lindane is now used with adequate results. Apart from 5 cases in 1961, no cases of typhus have been reported during the last decade. These five came from a case of Brill's disease.

Among other harmful Arthropods, *Ixodes ricinus* plays a role as a vector of spring-summer encephalitis. These ticks are controlled, though not systematically, by treatment with DDT and BHC.

Lesser problems are posed by other undesirable insects, such as bed-bugs, cockroaches and fleas. DDT resistance has been observed in both bed-bugs and cockroaches.

VECTOR CONTROL IN MALARIA ERADICATION

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Whenever malaria eradication is attempted through vector control, efforts should be made to assess the degree of control achieved and its effectiveness in producing a downward trend in malaria transmission.

"Vector control" refers here to reduction of the mosquito population's vectorial capacity,

defined as the incidence of infective bites distributed to man per case per day if the vector were completely receptive to infection. Control is epidemiologically effective when the vectorial capacity is such that the people cannot receive one potentially infective bite per existing case. A declining rate of transmission could be predicted from this finding.

Vectorial capacity as defined may be expressed as the product of three parameters:—(*a*) the incidence of biting-contact between the mosquito and the people, in bites per person per night. This *man-biting rate* represents the average number of females infected per case per day; (*b*) *the expectation of infective life*, or days of infective life per mosquito infected with the given parasite; (*c*) *the man-biting habit*, or bites on man per day per individual female.

The following table illustrates control of a population having a natural man-biting rate of 10, man-biting habit of 0·25, female daily survival-rate of 0·9 and transmitting *P. falciparum* with 12-day sporogony:—

	Proportion surviving per day	*Man-biting rate (bites)*	*Expectation of infective life (days)*	*Man-biting habit (bites)*	*Vectorial capacity*
Pre-attack	0·9	10·0	2·68	0·25	6·70
Attack (*a*)	0·8	4·72	0·308	0·25	0·364
(*b*)	0·7	2·96	0·0388	0·25	0·0287
(*c*)	0·7	1·48	0·0388	0·125	0·0072

Three possible effects of spraying are shown, supposing output from the breeding-places to be unaffected. In (*a*) and (*b*) the indicated reductions in daily survival entail the reductions shown in the man-biting rate and expectation of infective life; hence the much sharper reductions in vectorial capacity. Line (*c*) postulates a halved man-biting habit (by deviation to animals, as may be common under DDT), superimposed on reduced longevity. This, by halving also the man-biting rate, reduces vectorial capacity by a further 75%.

In terms of epidemiological effectiveness, in situation (*c*) the unit source could give rise to about one infective bite per 140 days (1/0·0072), which is probably below the critical malaria reproduction level even where most cases remain untreated. In (*b*) there could be one infective bite per case per 35 days—long enough to detect and treat most cases in a malaria eradication programme. Ineffective vector control is represented by (*a*), where the source could give rise to an infective bite about once in 3 days.

In the above examples the receptive vector's capacity to transmit *P. vivax* would be greater and the degrees of its reduction less, because of that parasite's quicker sporogony.

The problems of measuring vectorial capacity in field practice are essentially ones of sampling and scale. Direct biting-catches on human baits probably offer the best hope of estimating the incidence of contact with the people. I have discussed the difficulties of this measurement in an unpublished WHO document (WHO/Mal/450). For estimating the expectation of infective life the most helpful measurement is the proportion of parous females. Females caught biting man, as advocated by Hamon (3) are examined for uncoiling of the ovarian tracheoles. Computation of the expectation of infective life, using this proportion, is discussed by Garrett-Jones and Grab (2). Finally, the man biting habit is compounded of the mosquito's frequency of feeding and its human blood index. The collection of blood-meals presents formidable sampling difficulties, reviewed by Garrett-Jones (1).

Despite the difficulties it should be a primary concern of malaria entomologists to assess vectorial capacity and the resulting epidemiological trend. Its study demands priority as the operational criterion of insecticidal attack. Moreover, the problems involved constitute as strong a scientific challenge as may be encountered in most laboratory research.

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PROBLEMS IN ASSESSING THE TOXICITY OF INSECTICIDE-TREATED HOUSES TO MOSQUITOES

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There is no laboratory substitute for assessing the toxicity of an insecticide-treated house, because the habits of mosquitoes are important in assessing kill under field conditions. There are many problems in assessing kill but they are reduced by using experimental huts instead of local houses. The problems largely overcome and their means of solution are:

1. *Problem:* To make efficient collections of mosquitoes killed indoors by the insecticide. *Solution:* The experimental huts are of standard dimensions and collections are facilitated by white-painted floors, no fires indoors, and a bed as the only furnishing.
2. *Problem:* To assess the delayed mortalities of the proportion of mosquitoes that leave the treated house. *Solution:* Provided that the insecticide is non-irritant or non-repellent, delayed mortalities of *Anopheles gambiae* can be assessed efficiently by means of an exit window-trap fitting to the wall facing east.
3. *Problem:* To take into account that the persistence of toxicity of many insecticide formulations is greatly affected by the types of substrate of which the resting places are composed. *Solution:* The toxicity of an insecticide is assessed simultaneously in several huts lined with different materials. It is possible to state the toxicity of the insecticide at its best i.e. on non-sorbtive grass, and at its worst i.e. on sorbtive mud. Its toxicity under natural conditions would be expected to lie somewhere between these extremes depending on the extent of resting on the two types of substrate that occurs under natural conditions.
4. *Problem:* Insecticide-treated houses in East Africa are frequently infested with ants which seriously interfere with insecticide assessment because they drag away and devour the bodies of mosquitoes killed by the insecticide. *Solution:* Ant-entry is prevented by building the floor of experimental huts above ground level, on short concrete pillars surrounded by water.

Although the window trap-hut is perfectly adequate for assessing non-repellent insecticides against *A. gambiae*, recent studies with specially constructed huts have shown that this design is unsuitable for assessing the toxicity of insecticides to species such as *Mansonia uniformis* which, unlike *A. gambiae*, leave the hut largely during the night that they take a blood-meal, and through the open eaves. There is also evidence that the window-trap is less efficient when assessing irritant or repellent insecticides against *A. gambiae* because of greater egress occurring through the open eaves. This Institute is therefore currently experimenting with huts fitted with verandah-traps as well as window-traps to obtain more information on eave egress.

Another problem receiving attention is that there is no provision at present in insecticide trials for assessing the inhibiting effect that an insecticide may have on entry of mosquitoes into houses. This problem is being studied by means of specially built huts with ingress-traps fitted in the eaves and in windows.

GENERAL MEDICAL AND VETERINARY ENTOMOLOGY

STRUCTURE OF THE ANTENNAE AND MOUTHPARTS AS RELATED TO FEEDING HABITS OF *CULICOIDES* (DIPTERA: CERATOPOGONIDAE)

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The antennal segments of ornithophilic female *Culicoides* possess more olfactory sensilla than those of species known to prefer mammalian hosts.

Females of some of the non-haematophagous species possess rudimentary non-bloodsucking mouth parts while in other species the mouth parts appear to be secondarily reduced.

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REPRODUCTION IN MOSQUITOES OF THE HIGH ARCTIC*

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The mosquitoes, *Aedes* (*Ochlerotatus*) *impiger* (Walk.) and *A.* (*O.*) *nigripes* (Zett.), are common at Lake Hazen, Ellesmere Island (71° 18′ W, 81° 49′ N) (Oliver 1963). This high arctic site lies within 500 miles of the north pole, and within 150 miles of the northernmost latitude at which mosquitoes exist. Features of the phenology and reproduction of the mosquitoes are described here. Unless specified otherwise remarks refer to both species.

The eggs, in which one or more winters are spent, hatch at snow-melt, usually in early June. Emergence occurs 3-4 weeks later and shows a slight diel periodicity, correlated with

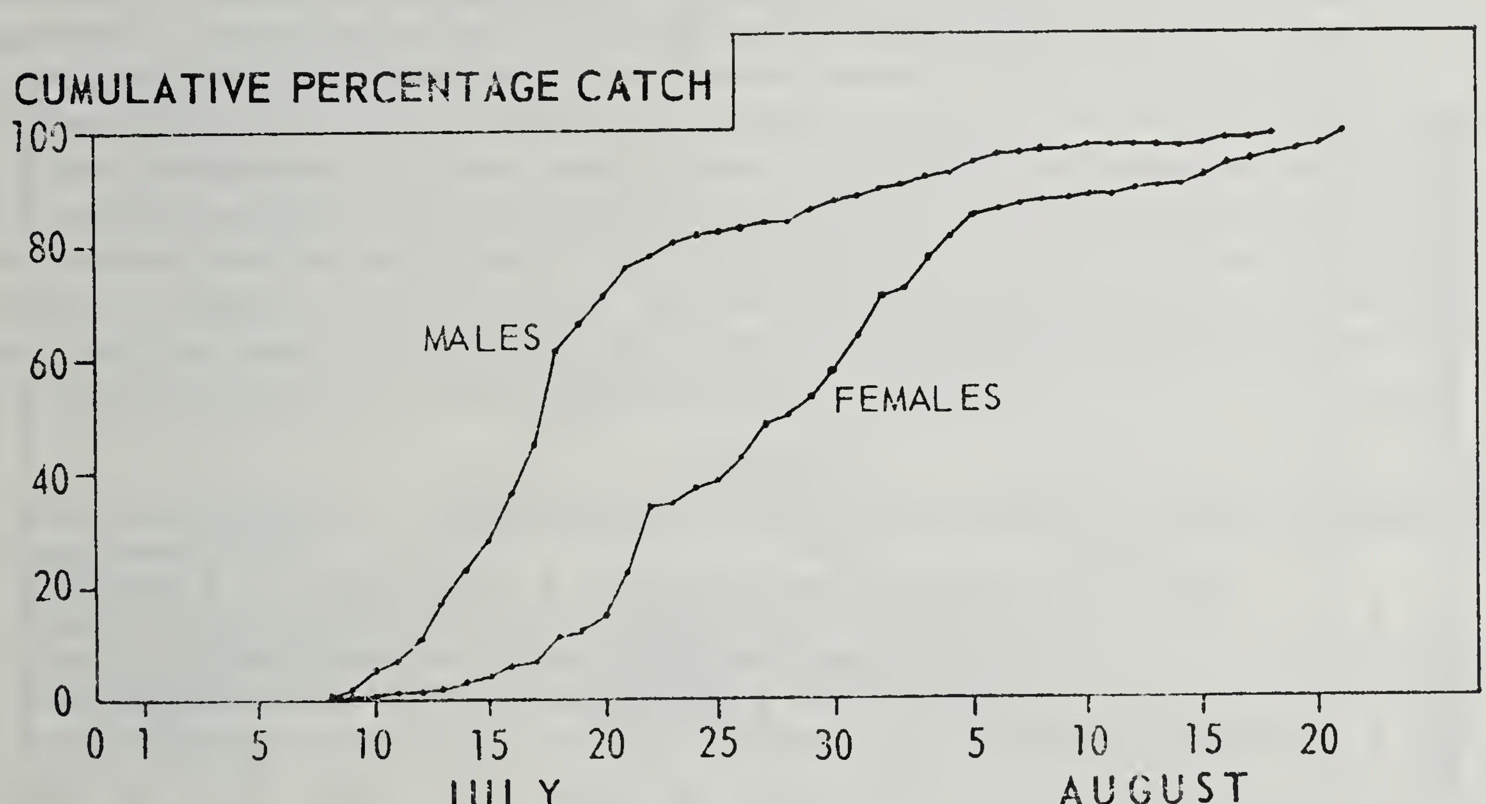

Fig. 1. The flying season of *Aedes nigripes* at Lake Hazen in 1963, shown by catches in a Visual Attraction Trap (Haufe and Burgess, 1960). Trapping began on 14 June and stopped on 21 August. The sample comprised 250 males and 1,243 females.

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water temperature. During their first 24 hours both sexes commonly take nectar (mainly of arctic avens, *Dryas integrifolia* (Vahl.) and bask on insolated surfaces, moving round so as to face the sun which remains continuously above the horizon between April and September. Males begin swarming in their second day. Virgin females visit swarms and are inseminated there. Mating has not been seen outside swarms. Females (usually after insemination) first seek blood on their second day as adults. In nature, during mid-July, females require 6 days or less (*A. impiger*) or 8 days or less (*A. nigripes*) after emergence to become gravid (Sella's stage 5). The average July screen-temperature is *ca* 44°F. (6·7°C.). After their first blood meal, females can lay up to 76 and 47 eggs, respectively; some return to bite at least once more. By mid-August, when snow begins to lie again, activity has already fallen to a low level (fig. 1).

Some females can mature and lay a first batch of eggs without a blood meal, when maintained on *Dryas* flowers and/or sucrose solution, though not when offered water alone. This type of autogenous ovarian development is associated with extensive, stepped resorption of oocytes such that sometimes only one finally matures and is laid. Follicles next to resorbed oocytes appear capable of subsequent development. It is therefore possible that autogenous females can mature a second, perhaps larger, batch on blood if able to obtain it. Since some females which come to bite in nature, but which are prevented from obtaining blood, can later lay eggs when maintained on *Dryas* alone, autogeny is probably developed facultatively in some individuals.

Females lay most eggs on northern margins of ponds, a preference especially marked in *A. nigripes*. This species oviposits 5-10 cm. above the current water level on a moist firm surface sheltered from wind but not from the sun. Females have never been seen laying except on surfaces directly facing the sun. As the eggs occur mainly in sites directly insolated between 11 and 13 hours, it follows that oviposition is periodic, with a peak near solar noon (fig. 2). Eggs are thus laid in those places which first become free of snow and ice the next spring when the eggs hatch.

Certain findings described here have been reported briefly elsewhere (1).

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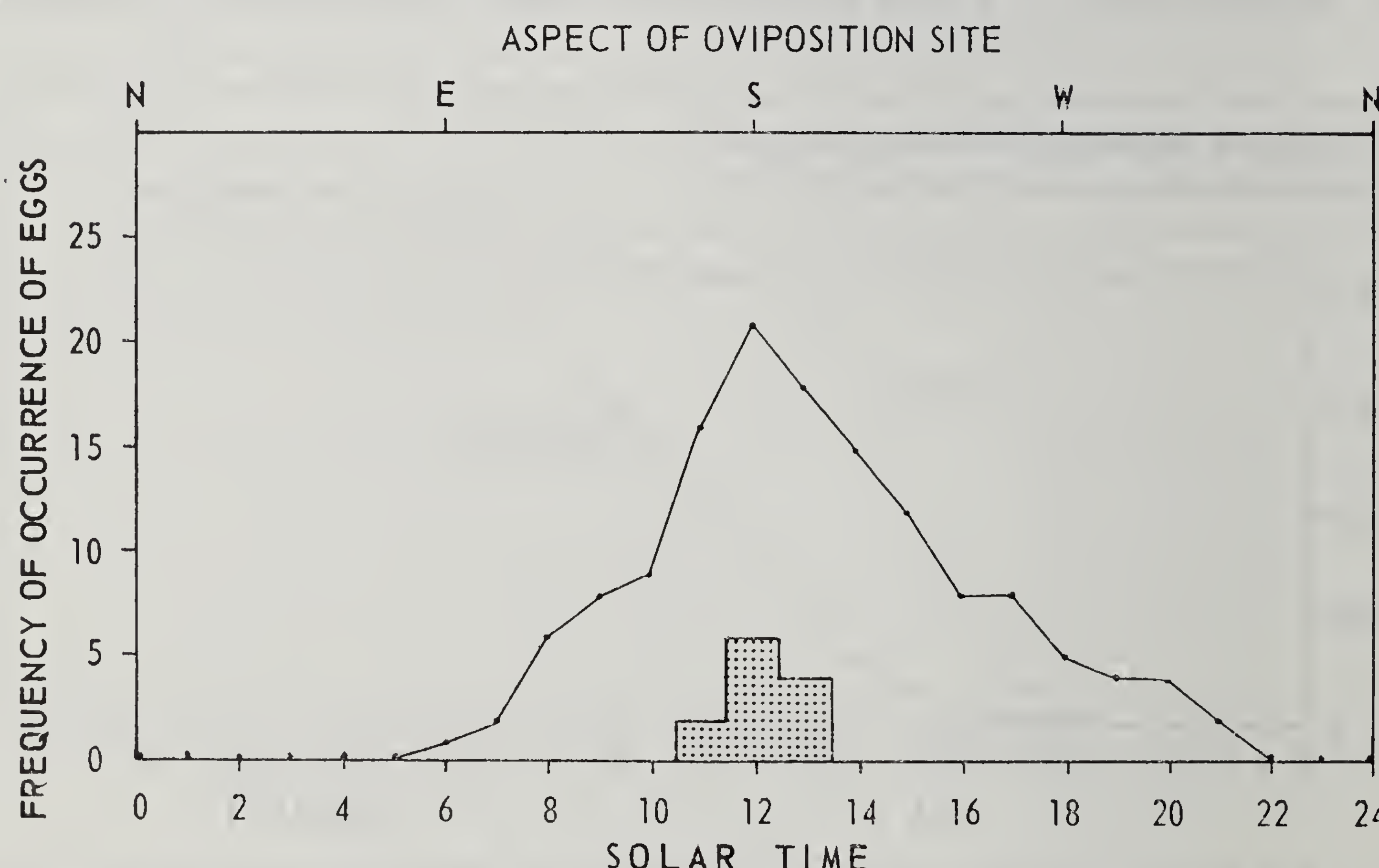

Fig. 2. The periodicity of oviposition of *Aedes nigripes* at Lake Hazen in 1963, shown by occurrence of eggs on sites with different aspects. The central, shaded histogram records occasions when maximum density of eggs could be unequivocally assigned to a single hour within the range. Observations were made in August 1963.

COLD TOLERANCE OF ADULT *CULEX TARSALIS*

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The mosquito *Culex tarsalis* overwinters as the adult female. As this insect is the principal vector of encephalitides in the western United States, it is important to understand the factors involved in successful hibernation. Eventually such knowledge may be used in forecasting populations to be encountered the following year, and to determine whether this mosquito can overwinter virus.

Mosquitoes tested were cultures developed from California (35°N) and from Washington (47°N), and Washington mosquitoes collected as pupae or larvae in nature. Larvae and/or adults were exposed to 8 and 16 hour daily photoperiods found to affect fat body size maximally (2), and to various temperature conditions. Females were tested, and these were fed sucrose only. They were placed in small plastic isolation chambers within a sealed jar containing humidity-regulating potassium hydroxide solution. Survival success was rated by time in days to achieve 50% mortality (LT_{50}) under specified exposure conditions.

As indicated by other investigators (1, 5) maximum survival occurs in a narrow temperature range near 0°C. When relative humidities of 20, 50 and 90% were compared, the highest of these was invariably most favorable. All hibernation exposures related here were therefore made at 0 or −2°C at 90% relative humidity. These temperature and humidity combinations rather parallel previous experiences with *C. tarsalis* and *C. pipiens* (3, 4).

Initial tests were made with the California strain. On 8 hour photoperiod maximum LT_{50} was 25 days, on 16 hour photoperiod the LT_{50} was 9 days. Because of low survival of the California strain a cold selection test was made to improve cold tolerance. Larvae and adults were reared at 22°C with 0° exposure for two days in both stages, progeny from the survivors receiving the same treatment. The object was to destroy approximately 80% and obtain progeny with improved cold resistance. At eleven generations the maximum LT_{50} was still 25 days.

Hibernation survival tests were conducted with the Washington strain. This laboratory culture, when reared on 8 hour photoperiod, had a maximum LT_{50} at 0°C of 73 days. Washington *C. tarsalis*, collected in nature as pupae or full grown larvae, showed a seasonal progression in cold tolerance. Collections of August 1, 14, September 10 and October 5, 1963 tested at 0°C and 90% relative humidity, demonstrated an LT_{50} of 52, 104, 102, and 115 days respectively. Average maximum and minimum temperatures for these three months were very similar.

From these and related experiments conducted it can be shown that for *Culex tarsalis*: (1) Short photoperiod increases cold tolerance. (2) Maximum survival occurs near 0°C. (3) A relative humidity near saturation favors survival. (4) Prior exposure to cold temperatures increases survival somewhat. (5) Genetically based differences occur in cold tolerance of strains originating from California and Washington. (6) Combinations of short photoperiod and low temperature provide maximum survival of the Washington culture, but there are still factors in nature which provide greater cold tolerance.

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MOSQUITOES AND DISEASE IN SARAWAK

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There are three main groups of diseases transmitted by mosquitoes in Sarawak; virus infections, malaria and filariasis. During two visits in 1962-63 and 1964 the aetiology of virus encephalitis was investigated. 100,000 mosquitoes of more than 100 species were collected during the investigation and the distribution and abundance of most of these have been correlated with topography and land usage.

VIRUS INFECTIONS. Tembusu virus was isolated from *Culex tritaeniorhynchus*, a strain of a virus of the Bunyamwera group from *Aedes curtipes*, and dengue virus from a hospital patient. Serological evidence shows that Japanese encephalitis and dengue are common everywhere, 90% of adults over the age of 15 having antibody to both. In Malaya and Singapore Japanese encephalitis has been isolated from *C. tritaeniorhynchus* and from *C. gelidus* (1, 2). Epidemiological evidence indicates that dengue is transmitted by *Ae. albopictus* and *Ae. aegypti.*

C. tritaeniorhynchus occurred widely in coastal and inland areas. In comparative catches its preferred host was poultry, but both pigs and man were readily bitten. One of the main breeding-places was rice-fields and a high population density was associated with the rice-growing season. *C. gelidus* was very common in areas of settled cultivation, often with *C. tritaeniorhynchus*, and its preferred host was pig. Whereas *C. tritaeniorhynchus* was common in forest villages where rice was grown, *C. gelidus* was not. *Ae. albopictus* was present in all the areas examined.

MALARIA. The main vector of malaria is *Anopheles leucosphyrus*, a mosquito which is found mainly inland, associated with forest and hilly country. On the coastal plain *An. leucosphyrus* is absent and malaria is not common. *An. sundaicus* was probably responsible for coastal malaria.

In 1952 a malaria pilot project was started (6), and in 1954 the project was expanded to cover the whole country. Malaria has now been reduced very considerably by DDT-spraying of houses. There is still transmission in parts of the interior, where communications and travel are very difficult. In some areas where malaria has disappeared and DDT-spraying has been stopped, *An. leucosphyrus* has become firmly re-established.

FILARIASIS. Filariasis due to *Wuchereria bancrofti* and to *Brugia malayi* has been reported from Sarawak (5), but no detailed work has been done. Bancroftian filariasis is not yet known from towns but there are foci in inland forest areas which might be comparable to those reported from Malaya (4). The vector in these inland areas is not known; it might be *An. leucosphyrus* (5).

The form of *B. malayi*, whether periodic or sub-periodic, has not yet been established; both forms may be present. Microfilariae were reported by Mr. J. Yong in night blood films from inland areas where none were detected in day films (5); these may have been periodic *B. malayi*, but confirmation is required. Recently a daytime blood survey was made in a coastal village and 67 out of 227 people, nearly 30%, had circulating microfilariae. This high rate, together with other circumstantial evidence, indicates that the parasite may be the sub-periodic form.

In this coastal area the most common man-biting mosquitoes were *Mansonia bonneae* and *M. dives*. Both species are major vectors of sub-periodic *B. malayi* (3).

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THE DISTRIBUTION AND BIOLOGY OF *ANOPHELES BALABACENSIS* IN THAILAND (DIPTERA, CULICIDAE)

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In recent years *Anopheles balabacensis* has been recognized as an important vector of human malaria in Southeast Asia. In Thailand, it was first found infected in 1956, and it has become increasingly clear that it is the major vector of human malaria in many of the forested foothills of the country. Most of the present studies were carried on at Khao Mai Kaeo, southeast of Bangkok. In this area of tapioca plantation and tropical evergreen forest, malaria, chiefly caused by *P. falciparum*, is hyperendemic. *Anopheles balabacensis* was found to be the principal malaria vector in the area, with a sporozoite rate of 8·7% at the height of the yearly population curve. This species was found to be highly anthropophilic, and exophilic. It also fed on monkeys supplied as bait, but not on large domestic animals. The females rested in forest vegetation during the day, and congregated in the vicinity of human dwellings before dark. They remained quiescent on the vegetation for some time before entering the dwellings to feed on the sleeping inhabitants. The females may rest for sometime on the inner and outer walls of the houses before and after feeding, but catches from houses sprayed with DDT indicate that they may successfully evade treated surfaces. Larval habitats in the study area were extremely diffuse in distribution. Typically they consisted of a small depression at the side of a forest stream, often the footprint of a man or animal in the sandy loam, which had filled by seepage from the nearby stream. Several unusual breeding sites such as rock pools and pits dug for the mining of sapphires, were found at Khao Mai Kaeo and elsewhere in Thailand. Very frequently the breeding sites were shaded by a spiny palm of the genus *Salacca*.

Several cases of chloroquin resistant *Plasmodium falciparum* malaria developed in members of the research team during the study at Khao Mai Kaeo. The currently recommended U.S. Army prophylactic drug schedule failed to offer protection to two American investigators involved in the study, nor could either of the individuals be cleared of parasites by the use of chloroquin. Quinine was effective in both cases. Failure of therapeutic doses of chloroquin were also noted in the local population. Khao Mai Kaeo is the third area in Southeast Asia where well documented cases of chloroquin resistant *falciparum* malaria have been found in which *Anopheles balabacensis* appeared to be the principal or only vector.

Neither residual spraying nor larval control seem to offer hope of satisfactory control of malaria in the forested areas of Thailand where *A. balabacensis* is a vector. The detection of chloroquin resistant *falciparum* infections in such areas likewise calls for extreme caution in the large scale use of drugs in control program. For military operations in *balabacensis* areas the use of protective clothing and repellents should offer some protection. The late feeding time and shy habits of *A. balabacensis* also indicate the use of mosquito nets while sleeping, for military and civilian populations in *balabacensis* areas.

THE REARING OF SIMULIIDS (DIPTERA)

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Continuous culture of simuliids indoors would aid in studying the biology and taxonomy of the different stages.

Eggs and larvae of certain species were readily collected from natural streams and returned to the laboratory in cool containers. However, in some Canadian species, e.g., *Simulium aureum* Fries, it was more reliable to obtain eggs from blood-fed, and presumably mated, females collected from chickens exposed in the forest canopy (2). Engorged females were kept in darkened boxes at 60°F (1), and fed on dry sucrose and water (3). After ten days. females were exposed to room temperature and dim light, and presented with grass blades floating on water. Usually eggs were laid on the wet edge of the leaf. Eggs were kept at

60°F, at least until the sclerotized head capsule showed through the shell or larvae hatched, and then were placed in artificial streams. Some eggs of *S. aureum* and all those of univoltine species, e.g., *Gymnopais* sp., entered a diapause, and at least a two-month storage at 33-40°F was required to break it. Thereafter these eggs were kept at 60°F until ready for rearing.

After testing many previous methods (4, 5), giving no better than 20% success, we developed the present apparatus. This consists of: (1) a filter containing 12 cu. ft. of highly activated granular carbon, sand and gravel, (2) a head tank, (3) troughs containing larvae, and (4) a device for dispensing a dilute yeast suspension (fig. 1). The rearing troughs in units of 10-11, were $\frac{1}{2}$ in. wide, 1 in. deep and 4 ft. long, each with a flat bottom and vertical sides and usually inclined at 1 in 36. Each pair of units (21 troughs) was supported, 2-3 ft. below the head tank, in a galvanized iron pan. To prevent larval escape, each trough was deepened into a reservoir (G) terminating in a stainless steel screen (100 mesh/in.). Filtered dechlorinated tap-water (A) entered each trough from a manifold (E) at a constant volume of flow set by the head tank. Each manifold, an acrylic plastic tube (diam. 1 in.), had a row of 1/16-inch holes, each fitted with a one-inch plastic tube supplying each trough. The little tubes were clear of the sides and bottom of the troughs preventing larvae from migrating into the manifold.

Baker's yeast was suspended in filtered water with a blender and kept in suspension in a flask with a stirrer. From there the suspension was diluted with more water in small tanks. Larvae were fed this dilute yeast (C) which dripped into each trough from a separate manifold (F). The feeding apparatus was frequently dismantled and cleaned without disturbing the water flow or larvae.

Adults of twelve Canadian species were reared from eggs or young larvae. The yield of *S. aureum* adults from eggs reached 80% and was usually over 50-60%. Even some larvae of *S. pictipes* Hagen, which inhabits large waterfalls were successfully reared.

Although no Canadian simuliid species has been bred indoors though a complete life cycle because of the mating, this may ultimately be accomplished since *Boophthora erythrocephala* de Geer was reared from pupae through two generations of mating and blood-feeding (6). However, oviposition and larval rearing were less successful with this species than we found with

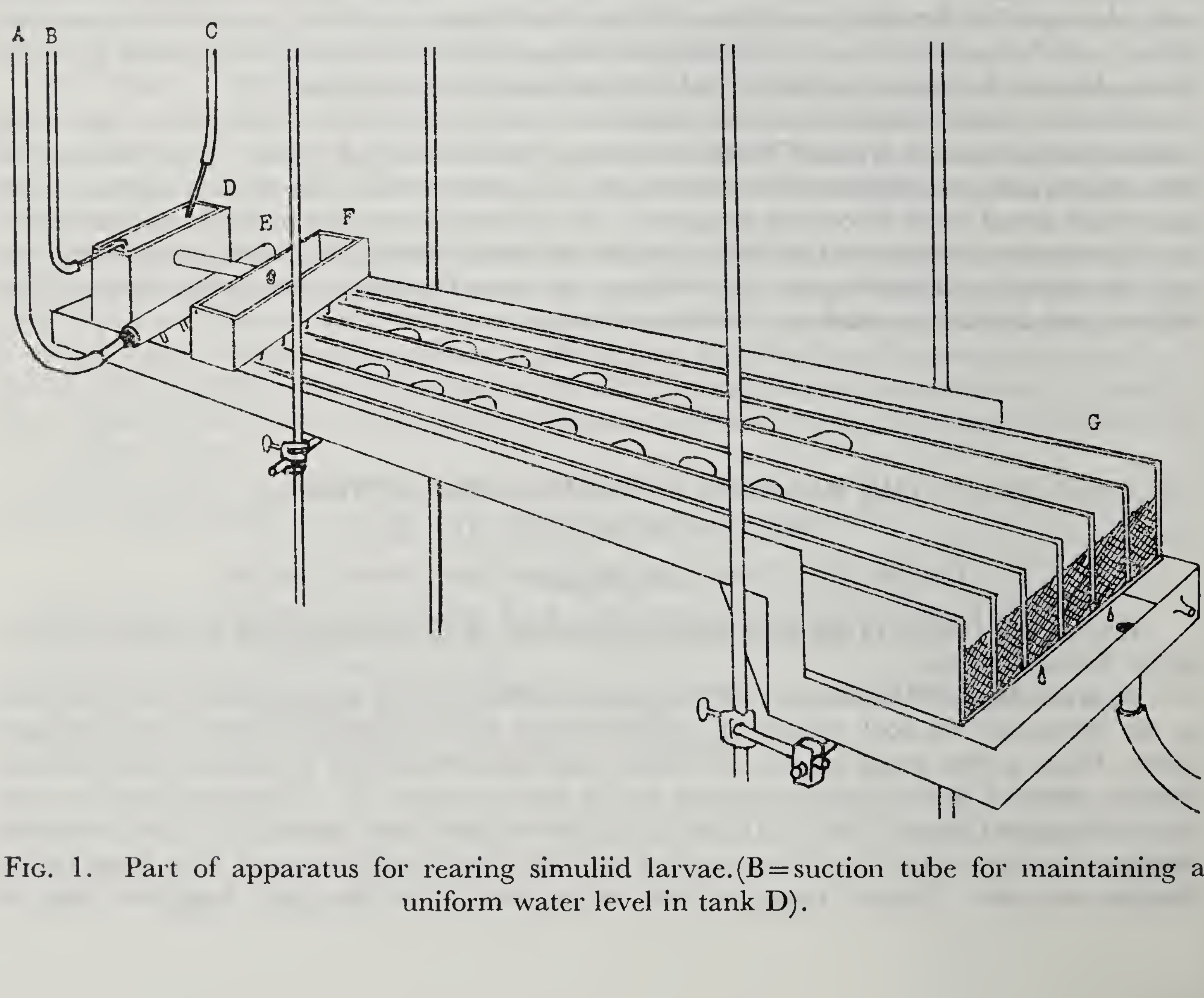

FIG. 1. Part of apparatus for rearing simuliid larvae.(B=suction tube for maintaining a uniform water level in tank D).

S. aureum. Preliminary experiments with artificial mating and egg fertilization will be reported elsewhere. The above apparatus for rearing simuliid larvae, with other techniques recently developed, gives promise of a more intensive study of black flies in the laboratory.

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RECENT STUDIES ON NON-ANTHROPOPHILIC *SIMULIUM DAMNOSUM* THEO. IN UGANDA

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Non-anthropophilic populations of *S. damnosum* are mapped showing a distribution through East, Central and South Africa, but not West Africa. Evidence that at higher altitudes *damnosum* becomes non-anthropophilic (3, 6), appears inverted in Tanganyika (8, 7), while in Uganda both forms occur throughout a common altitude range.

Studies were conducted at Kikagati and Kyansore Is. (4,200 ft.) on the Kagera R. (Uganda/Tanganyika border) where the population of *damnosum* is divisible into three portions, i.e. a very small number of man-biting flies, an enormous non-man-biting resting population of recently-emerged flies, and a portion intermediate in both numbers and habits which may land on dark surfaces but which do not bite man. The man-biting and intermediate portions can together be sampled using shade traps (4) although odour and sunshine determine sampling efficiency.

The resting and intermediate flies were shown not to be autogenous on the following grounds:—(*a*) Ovaries failed to develop on a diet of sultanas. (*b*) Although the fat-body tended to be large, the ovaries were never beyond Stage II. (*c*) There was clear fluid only in the crop; never in the gut (cf *Culicoides* (1)). (*d*) The man-biting and intermediate portions were composed of the normal proportions of parous and nulliparous flies to be expected from stable breeding conditions (10), therefore the resting portion did not revert to biting after the first ovarian cycle (2, 5).

Wing measurements (radio-median cross-vein to tip) were taken of anthropophilic samples from the Victoria Nile (mean temp. 24-25°C) and from the cold Ruimi R. flowing from the Ruwenzoris (mean 19-20°C); all surprisingly fell within the same small size range (1·725-1·745 mm.). Several samples of the three portions of the Kikagati population (Kagera R. mean temp. 22-23°C) showed however that the man-biting portion was composed of small flies (mean wing 1·688; 1·704 mm.), the resting portion of large flies (1·793; 1·817; 1·820 mm.) and the behavioristically intermediate portion of flies of intermediate size (1·737 mm.), these differences in mean measurements being highly significant.

However, wing lengths of Kikagati behavioural forms gave three separate peaks, while if they represented nutritional effects on larvae from the same cline, a single continuous curve would be obtained. It seems highly probable that intermediate behavioural forms could exist. These results do not rule out the possibility that *damnosum* may be autogenous at further extremes.

The wing lengths of all Kikagati samples come within the range of variation recorded (9) of man-biting samples in West Africa. While a large proportion of larvae from Kikagati showed a tendency towards reduction in the extent of coverage by integumental spicules, they fall within the normal range of variation. Otherwise the pupae and the adults of both sexes were indistinguishable morphologically from typical anthropophilic *damnosum*. There therefore

appears no means of separating different behavioural populations on morphological grounds.

It is concluded that as host preferences appear to be genetically determined consideration might be given to the non-anthropophilic portion being utilised in consolidation of control operations in replacement of the anthropophilic form following insecticide treatment. However, mixed non-anthropophilic populations must be treated as potential sources of re-infestation.

Dr. R. W. Dunbar (Durham) has found cytological evidence that the Kikagati population is genetically mixed.

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BIOLOGIE DES TABANIDAE DE NOUVELLE-CALEDONIA ET DES NOUVELLES-HEBRIDES*

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En Océanie francaise les Diptères Tabanidae ne sont représentés que dans les archipels mélanésiens: Nouvelle-Calédonie et dépendances (îles Bélep, Loyauté, île des Pins) et Nouvelles-Hébrides où dix-huit espèces sont actuellement connues (Mackerras et Rageau, 1958; Mackerras, 1962). L'étude de leur biologie n'a débuté qu'en 1954 et nous l'avons poursuivie jusqu'en 1959. Auparavant Williams (1943) avait signalé l'anthropophilie de *Dasybasis rubricallosa* (Ricardo, 1914) sur les plages de Nouvelle-Calédonie et de l'île des Pins. Cette espèce paraît la seule dont la femelle pique l'homme et présente un intérêt médical. Nous en avons observé tous les stades à Nouméa alors que la femelle seule était connue avant notre étude. Nous avons tenté l'élevage des larves et obtenu des adultes à partir des nymphes prises dans le sol. C'est une espèce littorale dont les stades préimaginaux vivent dans le sable des plages au-dessus du niveau des marées et dont les adultes s'écartent peu du rivage. Ces imagos apparaissent saisonnièrement, de fin septembre à avril-mai, avec une plus grande fréquence de décembre à mars, c'est-à-dire pendant les mois les plus chauds et les plus pluvieux. Les femelles assaillent les baigneurs et les pêcheurs lorsqu'ils sortent de l'eau et séjournent sur les plages et peuvent attaquer également les chiens et les chevaux. Leur piqûre est rapide et douloureuse mais ne laisse généralement pas de traces. Elle ne paraît transmettre aucun germe pathogène. L'horaire d'activité des femelles de *D. rubricallosa* est limité aux heures chaudes de la journée, entre 11 heures et 16 heures, par temps calme et ensoleillé. Elles cessent leurs attaques lorsque la température baisse ou que le vent s'élève. Les mâles s'observent plus rarement mais sont attirés de nuit par la lumière électrique dans les maisons au bord de la mer.

Les autres espèces de Tabanidae de Nouvelle-Calédonie ont également un rythme saisonnier et les imagos ne s'observent que de fin septembre à début mai. Les femelles n'ont jamais été trouvées gorgées de sang et nous ignorons leurs habitudes trophiques.

La plus commune est *Cydistomyia risbeci* Mackerras et Rageau, 1958 qui se rencontre fréquemment dans les maisons et paraît attirée par l'homme, les gros mammifères (chevaux, boeufs) et les voitures. Elle pénètre plus loin à l'intérieur de l'île que *D. rubricallosa*, jusqu'à 10 et même 20 km de la côte et s'observe en altitude jusqu'à 800 m au moins.

*Une étude plus détaillée a été publiée dans le Bulletin de la Société de Pathologie exotique (1964).

Philoliche neocaledonica (Mégnin, 1878) est une très grande espèce à très longue trompe, commune de décembre à mars-avril dans les vallées profondes et en montagne. Les mâles sont rares et la lumière artificielle ne les attire pas, à la différence de ceux des deux espèces précédentes. Les femelles, plus sauvages que celles de *C. risbeci*, peuvent voler autour de l'homme, des chevaux et des bovins, ce qui les a fait accuser sans preuves d'agressivité. Mégnin et Germain (1878) avaient même accusé cette espèce de transmettre le charbon bactéridien aux chevaux et à l'homme dans l'île des Pins. Les autres *Philoliche* (par ex.: *P. buxtoni* Mackerras et Rageau 1958) ont une biologie analogue.

Aux Nouvelles-Hébrides les Tabanidae sont représentés par *Cydistomyia veitchi* (Bezzi, 1928), forme nouvelle (?) et *Tabanus expulsus* Walker, 1854. Les femelles seules sont connues pour ces deux espèces et elles se rencontrent fréquemment dans l'île Tanna. Elles volent autour de l'homme et des chevaux mais ne paraissent pas les piquer. On ignore leurs préférences trophiques.

La faune des Tabanidae des Nouvelles-Hébrides est apparemment plus pauvre que celle de la Nouvelle-Calédonie et elle a été bien moins étudiée.

La lutte contre les Tabanidae hématophages n'a pas encore été entreprise en Nouvelle-Calédonie et aux Nouvelles-Hébrides où ces Diptères ne paraissent pas avoir de rôle pathogène Elle ne se justifierait que contre *Dasybasis rubricallosa* sur les plages fréquentées par les touristes. On se contente actuellement de moyens de protection individuels, par exemple l'usage de répulsifs. Pour réduire la densité des femelles on pourrait utiliser des pièges ou des brouillards insecticides. La destruction des larves serait peut-être plus rentable en raison de leur localisation à faible profondeur sur une étroite bande côtière. On pourrait expérimenter l'épandage de granulés insecticides à longue rémanence, à base de dieldrine notamment, sur un gîte larvaire aisément contrôlable (plage de l'Anse Vata près de Nouméa, par ex.) et en octobre, au moment de l'apparition massive des femelles.

PUBLIC HEALTH ENTOMOLOGY—THE STEPCHILD OF PROGRESS

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Public Health Entomology, the amorphous and immature offspring of Medical-Veterinary Entomology, is unique by virtue of its closeness to the people and their problems. In the United States most of these entomologists are employed by local or state health departments where the public has ready access to their services. They must be adept at public relations as it is necessary to establish and maintain good rapport with all types of community and academic groups or agencies. Their responsibilities include not only arthropod control, but also poisonous plants, bird and mammal control, or any other biological nuisance.

The public appears to be developing a hyper-awareness toward arthropods and their control as a result of a better standard of living, technological developments, and population growth. For example, concomitant with a rise in sanitation and personal hygiene is a growing feeling that it is no longer necessary to share living quarters with vermin such as cockroaches and bedbugs; furthermore, this better standard of living allows more people to have homes and gardens. An interesting adjunct of the latter is the current concern over spider bites. More work is necessary on spider biology and venom biochemistry.

The technological advances have created leisure time, in which to travel and visit woodland areas. Sylvatic ticks, like *Ornithodorus coriaceus* Koch, are bad biters and studies should be effected on their saliva or other reaction producing agents.

Modern technology has also developed the organic insecticides. People use and will continue to use these compounds despite the fact that there is much confusion regarding their uses and hazards. Public Health Entomology must respond to the requests of the public by supplying proper advice and adequate safety information.

Another problem confronting the health agency entomologist is population growth with complaints of flies from residents close to farms. The transition from agriculture to housing can be awkward, with the entomologist often in the middle trying to satisfy both parties. From stable or poultry ranch fly control, the problem changes to occasional complaints of fleas, cockroaches, carpet beetles, ticks, or other noxious insects. The public wants no nuisance, pest, or annoyance.

Public Health Entomologists, being so close and available, are contacted on many problems. It may be an actual insect invasion or an imagined condition formerly called Entomophobia, now known as Delusory Parasitosis. All requests, no matter how unusual, should get whatever assistance is feasible and possible.

The purpose of this paper has been to discuss the role and function of Public Health Entomology within the parent discipline of Medical-Veterinary Entomology. It would appear that this unit of study is fulfilling, to some extent, a direct, immediate and personal requirement of the public.

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NEW OBSERVATIONS ON EYE-FREQUENTING LEPIDOPTERA FROM S.E. ASIA

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An entomological investigation in 1958 offered the opportunity for recording adult feeding habits of noctuid moths collected from two different regions in Cambodia. The identification of the two species revealed that *Lobocraspis griseifusa* Hps. and *Arcyophora sylvatica* Bütt. are regular visitors and occasional blood feeders on eyes of water buffaloes and cattle (1, 2, 3). Another entomological expedition was carried out in 1963 to Chiengmai, Northern Thailand, in order to continue these field investigations. Collecting started on the 25th of June 1963 and was extended to the 25th of July; by the generous assistance of the Department of Agriculture, Bangkok, and the keen interest shown by Mr. Pichai Manichote it was possible to extend the investigations over a longer period, i.e. up to July 1964.

On our arrival at Chiengmai the rainy season had already started and progressed as our field investigations proceeded further. The flying period of the moths coincided with our arrival, and the number of moths collected per night increased constantly to the first days in July. From that date onwards it was very easy to collect several hundred specimens per night at a selected sampling site approx. 8 km North of Chiengmai. In addition collecting was carried out in a number of villages, and the results given in this paper refer to Mae Juac Cattle Breeding Station, the Zoological Garden of Chiengmai, the Horse Breeding Station, Chiengmai, a Forestry Camp along the Fang Road, and the Agricultural Research Station, Fang.

On the basis of the observations made in Cambodia we expected to find *Lobocraspis griseifusa* and *Arcyophora sylvatica* on bovine species only. However, we soon discovered that a pyralid, *Pionea damastesalis* Wlk., exhibited the same eye-frequenting behaviour as the two afore-mentioned noctuids. As a result of further investigations several other pyralids were discovered and at a later stage we found that geometrids were also involved in the same eye-frequenting behaviour. The results are summarised in Table No. 1. It is evident that a fairly restricted host specificity occurs in the noctuids whereas the pyralids show a very much wider range of preference covering various species belonging to the elephantidae, cervidae, suidae and equidae, as well as two species of bovidae.

TABLE 1

Eye-frequenting Lepidoptera and their Hosts. Investigations made in N. Thailand, June/July 1963

	BOVIDAE		CERVIDAE	SUIDAE	ELEPHANTIDAE	EQUIDAE	
	B. bubalis	*B. taurus*	*C. unicolor*	*S. scrofa*	*E. maximus*	*E. caballus*	*E. caballus* × *E. asinus*
NOCTUIDAE (*Westermanniinae*)							
Arcyophora sylvatica Bütt.	+ + +	+ + +	+ + +	–	–	–	–
Lobocraspis griseifusa Hps.	+ + +	+ + +	+ + +	–	–	–	–
(Misc. Species)							
Mocis undata Fabr.	–	–	–	(+)	–	–	–
Blasticorhinus rivulosa Wlk.	–	–	–	(+)	–	–	–
Nanaguna breviuscula Wlk.	–	–	–	(+)	–	–	–
Hypena conscitalis Wlk.	–	–	–	(+)	–	–	–
PYRALIDAE (*Pyraustinae*)							
Botyodes asialis Guenée	–	–	–	+	+ +	–	–
B. flavibasalis Moore	–	(+)	–	–	–	–	–
Filodes fulvidorsalis Huebner	–	–	+	–	–	–	–
Margaronia stolalis Guenée	+ +	+ +	(+)	+ +	–	–	–
Pagyda salvalis Walker	+	–	–	+	(+)	–	–
Pionea aureolalis Lederer	+	+	+ +	+	(+)	–	–
P. damastesalis Walker	+ + +	+ + +	+ + +	+ + +	+ + +	+ +	+ +
P. flavicinctalis Snellen	–	(+)	–	–	+ + +	–	–
Typsanodes linealis Moore	–	–	–	–	–	–	(+)
(*Hydrocampinae*)							
Bradina admixtalis Wlk.	(+)	+	–	–	–	–	–
GEOMETRIDAE (*Ennominae*)							
Hypochrosis korndorfferi Snellen	–	–	+	–	–	–	–
H. flavifusata Moore	+	+	–	+ + +	–	–	–
Peratophyga sp. nr. *tonseae* Debauche	–	–	–	(+)	–	–	–
Semiothisa fasciata Fabr.	+ +	+ +	+ +	+ + +	–	–	–
S. myandaria Wlk.	+	+	+ +	+	+	–	–
(*Sterrhinae*)							
Scopula attentata Wlk.	+	(+)	–	–	(+)	–	–
Somatina anthophilata Guenée	+	+ +	+	+ +	–	–	–
(*Geometrinae*)							
Pingasa chlora crenaria Guenée	–	–	–	(+)	+ + +	–	–
LYCAENIDAE (*Lycaeninae*)							
Lampides boeticus L.	–	–	–	(+)	–	–	–

Legend:
(+) = one record only, + + + = very common, + + = fairly common, + = occasional

The geometrids found indicate that there is not such a strict host specificity as in the noctuid species, *L. griseifusa* and *A. sylvatica.* Most of the geometrids were collected from several mammalian hosts, viz. buffalo, cattle, sambar, pig and elephant. The horses and mules were frequented by *Pionea damastesalis* only, and a single record of *Typsanodes linealis* was taken from the mule. The only lycaenid species, *Lampides boeticus,* was collected from the domesticated pig.

[These observations are being published in more detail in Verhandl. Naturf. Ges. Basel.]

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EINFLUSS DER UMWELTFAKTOREN AUF DIE WIRTSPEZIFITÄT DER KLEINSAÜGERLÄUSE (ANOPLURA)

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Die früheren Ansichten (z.B die Fahrenholz'sche Arbeitshypothese), welche die strenge Spezialisierung der Läuse auf einen bestimmten Wirt betonen, sind irrtümlich. Sie überschätzen bedeutend die Spezialisierung der Läuse und halten sie für den einzigen Moment, der das Verhalten der Läuse vorbehaltslos festlegt. Dabei sind die auf die Läuse aus der äusseren Umwelt einwirkenden Einflüsse vollkommen übersehen worden. Bei den Läusen gibt es ohne Zweifel eine Spezialisierung auf den Wirt, diese Spezialisierung ist aber bei verschiedenen Arten verschieden entwickelt. Es gibt Arten, die auf einen bestimmten Wirt wirklich streng spezialisiert sind (z.B. *Hoplopleura longula* Neum. und *Polyplax gracilis* Fahr., die nur die Zwergmaus *Micromys minutus* parasitieren). Bei anderen Arten ist die Spezialisierung in ähnlich hohem Grad entwickelt, sie einschliesst jedoch schon einen bestimmten Kreis von phylogenetisch nahe verwandten Wirte (z.B. *Schizophthirus pleurophaeus* Burm., der nur die Bilche parasitiert). Für die Arten dieser zwei Gruppen ist es typisch, dass es sich einerseits um nur selten vorkommende Läuse handelt, andererseits dass ihre Wirte entweder sehr spezialisiert leben (Bilche) oder selbst selten und in der Natur nie in grosser Anzahl vorkommen. Beide diese Umstände setzen die Möglichkeit des Überganges der Läuse auf andere Wirte bis zum Minimum herab. Die hohe Spezialisierung dieser Läuse ist also eigentlich sekundär und ist durch die Einflüsse der äusseren Umwelt verursacht. Die dritte Gruppe bilden Läuse, die dem Leben auf einem breiteren Kreis der verwandten Wirte angepasst sind. In Abhängigkeit von der verschiedenen Zusammensetzung der Kleinsäugerfauna eines bestimmten Gebietes konnen diese Arten eine grössere Anzahl von Wirte parasitieren. Hierher gehören z.B. die gemeinen Arten *Hoplopleura acanthopus* Burm. und *Polyplax serrata* Burm. Diese Arten leben an Wirten, die in der Natur in grosser Anzahl vorkommen und oft in engen gegenseitigen Kontakt kommen und deshalb besitzen diese Läuse einen breiten Wirtskreis (es muss sich natürlich um mehr oder weniger phylogenetisch verwandte Wirte handeln). Ihre Spezialisierung kann man als **dynamische Spezialisierung** bezeichnen.

Bei den Läusen kann man auch gewisse Anzeichen der Zonenverbreitung, welche in Einzelheiten bei den Flöhen durchgearbeitet wurde, feststellen. Oft ist sogar eine vollkommene Analogie zu beobachten. Bei den Flöhen ist z.B. die Zone der Aphanipteren des Eichhörnchen, wohin Eichhörnchen und alle Bilche gehören, entwickelt. Auch bei den Läusen ist diese Zone sehr deutlich ausgeprägt und ihre typischen Läuse sind *Neohaematopinus sciuri* Jancke, *Enderleinellus nitzschi* Fahr. und *Schizophthirus pleurophaeus* Burm. Ganz ähnlich ist auch bei den Läusen die Zone des Wildkaninchens ausgeprägt.

Die Wirte der Läuse kann man in drei Gruppen einteilen:

1. Als **Hauptwirt** ist solcher Wirt zu bezeichnen, welchen die Laus regelmässig parasitiert, saugt auf ihm und auf welchem auch die ganze ihre ontogenetische Entwicklung durchlaufen kann. Diese Wirte leben in freier Natur meistens in grosser Anzahl. So sind z.B. die Hauptwirte von *Hoplopleura acanthopus* die Wühlmäuse *Microtus arvalis, M. agrestis* und *Clethrionomys glareolus.*

2. Als **Nebenwirt** ist solcher Wirt zu bezeichnen, welchen die Laus unter gewissen Umständen parasitiert, allerdings im kleineren Ausmass als den Hauptwirt, auf welchem sie saugt und auf welchem auch ihre ontogenetische Entwicklung durchläuft. In der Natur kommen sie meistens nicht massenhaft vor. Alle mitteleuropäischen Wühlmäuse im engeren Sinne des Wortes (hauptsächlich *Pitymys subterraneus*) können die Nebenwirte von *Hoplopleura acanthopus* sein.

2. Als **Zufallswirt** ist solcher Wirt zu bezeichnen, auf welchem die Laus nur zufällig und vereinzelt vorkommt. Sie hat zu ihm keine engere Beziehung, sie saugt auf ihm nicht und auch ihre ontogenetische Entwicklung kann auf ihm nicht durchlaufen. Die Laus kann sich auf diesem Wirt nie längere Zeit erhalten. Die Arten der Gattung *Apodemus* sind z.B. die typischen Zufallswirte der Laus *Hoplopleura acanthopus.*

Bei den hochspezialisierten Läusen fällt diese Einteilung der Wirte selbstverständlich ab.

UNE DIFFUSION INSOUPCONNEE DU *SCLERODERMA DOMESTICUM* LATR. DANS LES HABITATIONS DE LA VILLE DE GENES

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Bien que depuis quelque temps on eut remarqué à Gênes des cas sporadiques de piqûres par *Scleroderma domesticum* Latr.; c'est cependant seulement en ces dernières années que ce fait a pris des proportions insoupçonnées.

Au printemps du 1956 j'avais été frappée par une invasion non commune de Sclerodermines dans deux maisons de Gênes et surtout par les singulières et remarquables manifestations que leurs piqûres avaient causées aux habitants. A partir de ce moment j'eus le hasard de voir d'autres cas d'une certaine importance, qu'auparavant je n'avais jamais observés, et que je pense brièvement rapporter.

Mr. A., qui habite au centre de Gênes, se présenta dans mon laboratoire assez préoccupé à cause d'un persistant et ennuyeux érithème qui déja depuis beaucoup de temps l'affligeait; cet érithème était peut-être relié, me dit il, aux piqûres d'une petite fourmi dont il avait capturè quelque exemplaires entre les draps de son lit et qu'il me donna en examen.

Je pus facilement constater qu'il s'agissait de la femelle du *Scleroderma domesticum* Latr.

L'alteration cutanée était vraiment considerable: Mr. A. presentait en certaines parties du corps des échymoses tels que je n'avais jamais observé en aucun cas de piqûre d'hyménoptére en general et de Béthilide en particulier.

A ce phénomène se joignit des considerables ennuis du système nerveux qui avaient provoqué dans le sujet une inquiétude et une situation psychique telle qu'il l'engagea non seulement à se débarasser des meubles vermoulus, mais aussi à quitter son logement.

Un autre cas considerable se rapporte à Mme. B. qui habite elle-même au centre de Gènes; elle fut, pendant cinq ans, tourmentée par des douloureuses piqûres, suivies par des érithèmes très développés avec parfois une légère alteration de la temperatue et du système nerveux. Tous ces phénomènes, n'étant pas reliés aux piqûres, venaient attribués aux causes les plus différentes.

Ce fut par hasard que Mr. B. réussit à capturer dans son logement le supposé agent blesseur identifié ensuite comme *Scleroderma domesticum* Latr. Dans le logis en question il me fut facile de résoudre la question qui depuis plusieurs années affligeait la famille B.: les meubles et d'autres objets en bois, complétament criblés par les larves des Anobiides, donnaient abri en enorme quantité au *Scleroderma domesticum* Latr.

Cependant ce qui causa l'alarme dans la population et mit en relief une diffusion vraiement insoupçonnée de Sclerodermines dans la ville de Gênes fut un article qui avait paru, sous le titre "Insetti che aggrediscono l'uomo e vivono nelle poltrone di casa", dans un journal de Gênes le 23 Mars 1963.

Le même matin le téléphone de mon bureau sonna presque sans interruption, c'etait des personnes qui, soupçonnant avoir dans leur logis l'insecte incriminé et d'avoir été piquées par lui, me soumettaient les questions les plus diverses que, naturellement je ne pouvais pas résoudre sans l'examen de l'agent vulnérant ou du moins supposé tel.

Je pus de telle façon constater qu'il y avait le *Scleroderma domesticum* Latr. dans beaucoup de maisons, au centre et en la banlieu de Gênes, et qu'ils étaient parfois assez nombreux.

Ce fait peut sembler étrange, cependant, malgré cette remarquable invasion de Sclerodermines, les sujets qui furent relier à cet insecte les manifestations, pathologiques dont ils étaient affligés furent très peu nombreux.

LIFE CYCLE OF *ECHIDNOPHAGA GALLINACEA*

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Based on their behaviour most Siphonaptera, including about 1,300 species, belong to one group. These fleas, such as *Xenopsylla cheopis*, are relatively independent from their host. A further two groups, comprising 70 species, can be distinguished. First the *Tunga*-type, in which the females develop into proper "endoparasites". Secondly the sticktight-type to which group belongs *Echidnophaga gallinacea*. The females of the latter group also become stationary parasites. In this paper, the development and biology of *Echidnophaga gallinacea* are described and compared with the corresponding data of *Xenopsylla cheopis* and *Tunga penetrans*.

1. *Development and biology*: Rate of development as well as optimal ecological conditions are similar for all three types of fleas. The mouthparts of the females of the sticktight-type are strongly developed because they have the additional function of anchoring the flea to the skin of the host.

2. *Biology and behaviour*: In contrast with other fleas, *Echidnophaga gallinacea* always shows a positive phototropism. This may account for their preference for the featherless areas of the chicken heads. In all species studied, copulation takes place only when the female has reached a certain degree of maturity after several blood meals. Place and position during copulation is different for each of the three groups. Oviposition begins immediately after copulation and is interrupted as soon as the sperms in the spermatheca are used up. "Free-living" fleas can act as vectors of plague, relapsing fever or helminthic infestations. Attached fleas usually do not play an important role as vectors, as they generally do not leave their hosts.

The adults of *Echidnophaga* attack only certain regions of their hosts. The blood supply in the host skin and the positive phototropism of the parasites may be responsible for this. The female of *Echidnophaga* does not penetrate the skin of the host as does the female of *Tunga*. *Echidnophaga* spend a relatively short time on the host, *i.e.* males about a week, females up to six weeks.

Comparison of *Echidnophaga* with *Xenopsylla* and *Tunga*	free type, e.g. *Xenopsylla cheopsis*	stickfast-type, e.g. *Echidnophaga gall.*	Tunga-type, e.g. *Tunga penetrans*
Size of mouth parts	♀ and ♂ normal	♀ much increased ♂ normal	♀ and ♂ normal rather small
Function of mouth parts	piercing skin of host for blood meal	bloodsucking and fixation to the host	blood sucking
Blood meals	♀ and ♂ periodically with certain intervals	♂ periodically ♀ permanent	♂ periodically ♀ permanent
Hatching of adults	♀ 3-4 days before ♂	♀ 3-4 days before ♂	♀ 1 day before ♂
First copulation	about 3 days after the females have hatched and reached a certain maturity		
Site of copulation	nest, skin or feathers of the host. Both partners are mobile	on the host ♀ sticking to host	on the host, after complete penetration of ♀
Localization	host and his nest	♀ on host ♂ on host and his nest	♀ on host ♂ on host or his nest
Preferred areas	whole body	areas with good blood supply mostly exposed to light	horny parts of skin
Phototactic behaviour (*a*) hungry adults	males and females positive		
(*b*) well fed adults	♀ and ♂ negative	♂ negative ♀ positive	♂ negative ♀ fixed permanently
Change of individual host	♀ and ♂ frequent	♀ occasionally ♂ capable	♀ never ♂ capable
Transmission of microorganisms	Pasteurella pestis trypanosomes helminths	possibly P. pestis Rickettsia prowazeki	none

BIOCHEMICAL STUDIES ON HYPERSENSITIVITY TO FLEA BITES

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Studies were conducted towards the isolation and characterization of the flea allergen present in the oral secretion of the cat flea (*Ctenocephalides felis felis*). Dialysis, and gel filtration using Sephadex G-50 and G-25, indicated that the allergen is of low molecular weight (below 4,000). It is stable to heat (105°C for 24 hours), and to acid conditions that hydrolyze proteins to their amino acid constituents (6N HCl, 105°C for 24 hours).

Induction of hypersensitivity to flea bites was found to be contingent upon conjugation of the hapten to the host's skin. Fractionation of skin from guinea pigs previously exposed to flea bites showed that the hapten was bound to the collagen fractions, i.e. tropocollagen (collagen soluble in neutral salt solutions) and acid soluble collagen. The identity and purity of these proteins was ascertained by amino acid analysis and by electron microscope examination.

Quantitative studies indicated that on a molecular basis, tropocollagen combined with more flea hapten than did acid soluble collagen. This is explained on the basis of the greater availability of reactive groups on the tropocollagen molecule than on the fully reconstituted collagen molecule. Acid soluble collagen, however, was found to serve as a better immunological carrier for the hapten than tropocollagen.

On the basis of the above it is proposed that upon its injection by the flea into the host's dermis the flea hapten reacts with tropocollagen molecules. When the molecules carrying the hapten proceed to form collagen fibrils, a full antigen is formed which in turn is responsible for the induction of hypersensitivity to flea bites.

SEX DIFFERENTIALS IN THE SPEED OF PRE-IMAGINAL DEVELOPMENT IN IXODID TICKS

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In spite of the absence of external sexual dimorphism in the pre-imaginal stages of ticks, males and females already differ biologically at these stages. Sex differences in the duration of the larval quiescence of two species of ticks (*Hyalomma dromedarii* and *Rhipicephalus sanguineus*) and in that of the nymphal quiescence of four species (*R. secundus* and *H. marginatum*, in addition to the two previous ones) were investigated. Statistically significant sex differences were observed in the duration of the larval quiescence of one species (*H. dromedarii*) and in the nymphal quiescence of all four species. In the case of the larval quiescence, as well as in that of the nymphal quiescence of three of the species, the development of the individuals which ultimately proved to be males was slower than that of "females"; but in one species, *H. marginatum*, the nymphal quiescence of the females was longer than that of the males. These sex differences in the nymphal quiescence are of the order of 1-2 days, as against an average duration of the quiescence of about 2-3 weeks. The observed sex differential in the larval quiescence (*H. dromedarii*) is only four hours, as against the average quiescence of 8-10 days.

But sex is not the only factor affecting the duration of the quiescence, even under constant physical conditions. Differences in average duration of quiescence of the offspring of different females, and after feeding on various hosts, are as large as the observed sex differentials. Individuals belonging to a single batch of uniform history scatter widely in the length of their quiescence. Furthermore, the duration of the larval and the nymphal quiescences of some individuals are apparently positively correlated. However, the sex differential reappears within almost every batch of individuals which had been kept under uniform conditions, whatever these conditions were.

The existence of a sex differential in the larval and nymphal quiescences can be understood

in view of differences in the internal morphology of nymphs of different sex already appearing at emergence. The occurrence of the processes of oogenesis and spermatogenesis during nymphal quiescence, as against the absence of such stresses on the organism during larval quiescence, explains perhaps why the sex differential is much more marked in the nymphal quiescence than in the larval quiescence. But no explanation can be offered for the fact that in some species the speed of development of the male is slower than that of the female, while in another species the opposite is true. It may however be mentioned that similar inconsistencies have been noticed in the direction of the sex differential in the speed of development of pre-imaginal stages of insects and even in the length of gestation of male and female embryos by mammals.

PAPERS READ IN TITLE

The following papers were either received too late for inclusion in the Programme or the authors were unable to attend the Congress.

THE HOLARCTIC SPECIES OF THE GENUS *THERONIA* (HYMENOPTERA ICHNEUMONIDAE)

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The genus *Theronia* contains medium-sized ichneumon-flies that are usually parasitic on the larvae and pupae of Lepidoptera. It is very well represented in the Oriental, Australasian, Ethiopian and Neotropical Regions, but is poorly known from the Palaearctic and Nearctic Regions. In the Palaearctic region there are only two species, *viz.*, *T. atalantae* (Poda) and *T. laevigata* (Tschek), while in the Nearctic region four species have been recorded: *T. atalantae* (Poda), *T. hilaris* (Say), *T. septentrionalis* (Krieger) and *T. bicincta* (Cresson). Of these, *T. bicincta* and *T. septentrionalis* are related to the Neotropical species in having a strong apical transverse carina on the propodeum. This feature separates the "Neotheronia" group of species centered in the Neotropical region. The rest of the Nearctic and the Palaearctic species are related to the Oriental species and form a distinct species group, the Atalantae Group, characterised by having the mandibular teeth of equal length, clypeus slightly raised basally, without any swellings, carina between antennal sockets weak or absent, areola always closed behind, ovipositor cylindric near apex, valves meeting in a straight line, not overlapping each other, lower valve of ovipositor with slanting saw-tooth-like ridges, upper valve without ridges, and the prepectal carina distinct to anterior margin of mesopleurum. The last mentioned feature separates the Atalantae Group from the Oriental species groups, for in the latter groups the prepectal carina is distinct on lower half of mesopleurum only and erased above with very few exceptions in which case the clypeus is not as described above. The Atalantae Group belongs to the subgenus *Theronia*. Five subgenera (*Theronia*, *Parema*, *Nomosphecia*, *Augerella* and *Epitheronia*) were recognised (1), based on a comparative study of the ovipositor, mandibular teeth and the prepectal carina. The subgenus *Theronia* is the most generalised and widely distributed amongst them.

The species of the Atalantae Group show differentiation in colour and can be divided into regional subspecies showing allopatric distribution. *Theronia* (*T.*) *atalantae* has three subspecies: *T.* (*T.*) *atalantae atalantae* (Poda) occurs widely in Europe; *T.* (*T.*) *atalantae gestator* (Thunberg) (= *T. japonica* Ashmead) in the Eastern Palaearctic region (I have seen specimens of it from Japan, Korea, Manchuria and Siberia), and *T.* (*T.*) *atalantae fulvescens* (Cresson) is widely distributed in North America. *Theronia* (*T.*) *laevigata* has so far been known from only two subspecies: *T.* (*T.*) *laevigata laevigata* (Tschek) from Europe and *T.* (*T.*) *laevigata nigra* Uchida from Eastern Palaearctic region (I have seen specimens of it from Japan and Siberia). *Theronia* (*T.*) *hilaris* (Say) from North America is extremely similar in morphology to *T.* (*T.*) *laevigata* and is probably to be considered a synonym of it. The American specimens are distinct in colouration and appear to represent a distinct subspecies, *T.* (*T.*) *laevigata hilaris* (Say).

The Atalantae Group of subgenus *Theronia* would thus contain two Holarctic species, *T.* (*T.*) *atalantae* and *T.* (*T.*) *laevigata*, each represented by three subspecies, one each from the Western Palaearctic region, the Eastern Palaearctic region and the Nearctic region. It would be of interest to collect them intensively in the Palaearctic region and know of the zones of intergradation between the Western and Eastern Palaearctic populations. This study supports the general thesis that the faunas of the eastern and western parts of the Palaearctic Region are related but distinct.

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THE DEVELOPMENT AND PRESENT STATUS OF INSECTICIDE RESISTANCE IN INSECTS IN CZECHOSLOVAKIA

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Since 1956, when DDT resistance in houseflies was found in East Slovakia, resistant strains of houseflies have been found in many localities, mainly in South Slovakia, Moravia and East Slovakia (2). A report of the status was given in 1961 (3). Since then, resistance in flies has not spread to other parts of the country. Resistance in houseflies to BHC is quite exceptional (two observations), resistance to organophosphates has not yet been observed.

In 1963, resistance to DDT was discovered in bedbugs, in 1964 strains of cockroaches (*Blatta orientalis*) were found resistant to DDT and/or dieldrin, the latter insecticide never being used in Czechoslovakia. In one case DDT tolerant Anopheline mosquitoes were found. The resistant strains of bedbugs and cockroaches are, however, very rare.

Considering the surprisingly slow development of insecticide resistance in Czechoslovakia, it seems worthy of note that resistance is quite common in surrounding countries. It is therefore, improbable that climatic conditions could be of importance in its development. It seems that the main cause of slowness of the development is the proper use of insecticides by trained personnel, limitation of their daily use to really necessary cases and the comparatively good hygiene, which themselves limit the development of insects.

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BEHAVIOR-GENETIC ANALYSIS OF INSECT POPULATIONS

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Knowledge of genome architecture, neuroendocrine functioning, sensory analyzers, and behavior patterning now permits behavior-genetic analyses of natural units in the organization, evolution, and adaptation of species populations. Our picture of the mosaic nature of the genome, that has emerged from the elegant *Drosophila* studies of the past half century, today appears to have considerable generality among bisexual species. Selection, inbreeding, hybridization, and backcrossing permit us to vary the balance and composition of the neuroendocrine, sensory, and motor mechanisms integrating the components of behavior patterns now being articulated in such exquisite detail by ethological analysis.

Classical genetics produced a mosaic picture of genome architecture to which Dobzhansky (2) has added the ingredient of integration and coadaptation. Behavior-genetic analyses may now help to uncover, at various levels of biological organization, some of the important units that have been linked together in developmental chains by evolution. Ethological behavior pattern analysis followed by the measurement of component trait distributions in populations, directional and stabilizing selection for variations in the expression of each trait, inbreeding to fix these variations, hybridisation, and (where possible) chromosome analyses are the empirically validated methods which can sharpen our focus sufficiently for us to identify natural units at various levels of organization. Furthermore, we may also begin to distinguish those units which segregate independently from others which assort in close interactive association.

Geotaxis appears as a component of activity, exploration, and foraging behaviors in many invertebrates. It had long been assumed that under a given set of conditions the sign of a taxis is an invariant property of a species (1). We have developed apparatus which places no restriction on the sign of the taxis (6). It affords objective and automatic measurements of both positive and negative geotactic behavior in *Drosophila* populations under a single set of

stimulus conditions as well as reliable mass screening measurements of individual differences in the expression of each.

Selective breeding over 140 generations and inbreeding for more than 30 generations have produced strains of flies showing oppositely skewed geotactic response distributions under physically identical stimulus conditions. As the next step in a natural unit analysis, chromosome assays have revealed that the three major *melanogaster* chromosomes have responded to selection in different ways. A further analysis (still in progress) appears to be showing substantial independence in the assortment of the three chromosomes and in their expression in geotaxis.

Phototaxis also appears as a component in the behavior patterns of many organisms (9). Selective breeding analysis (5) under one set of conditions has shown a substantial heritability for individual differences in the expression of this trait. Recently, apparatus has been developed for studying phototaxis analogous to that so successfully used with geotaxis (4). In confirmation of the previous phototaxis study, selection in the more sophisticated apparatus has again produced divergent strains that may now be further analysed.

Bidirectional selection for extremes as well as stabilising selection has produced similar results with optomotor thresholds (8). Apparently at this time we do not know of any behavioural traits in any species for variations in the expression of which selective breeding might not be possible (3); even the complex mating duet can be selected for alacrity (7).

The next step in the study of natural units will be the experimental synthesis of populations of individuals having known performance capacities on a series of traits and covering the range of possible combinations of abilities. Further analysis may then reveal the chromosome organization of this spectrum of genotypes as well as the critical sensory, motor and neuroendocrine components (natural units?) involved in the variations in capacity.

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